SOCIAL ASPECTS OF CALL LEARNING IN THE ZEBRA FINCH (TAENIOPYGIA GUTTATA) AND THE BUDGERIGAR (MELOPSITTACUS UNDULATUS)

Paul Bartlett

A Thesis Submitted for the Degree of PhD
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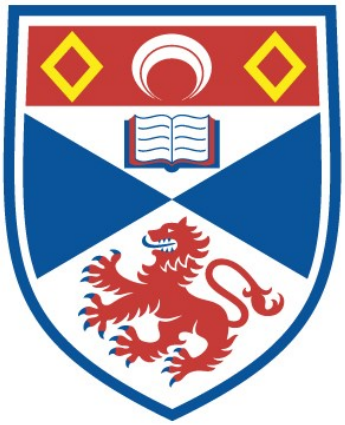

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by

Paul Bartlett

Submitted in fulfilment of the requirements
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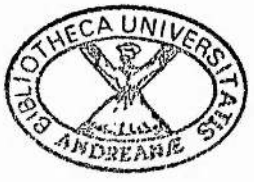

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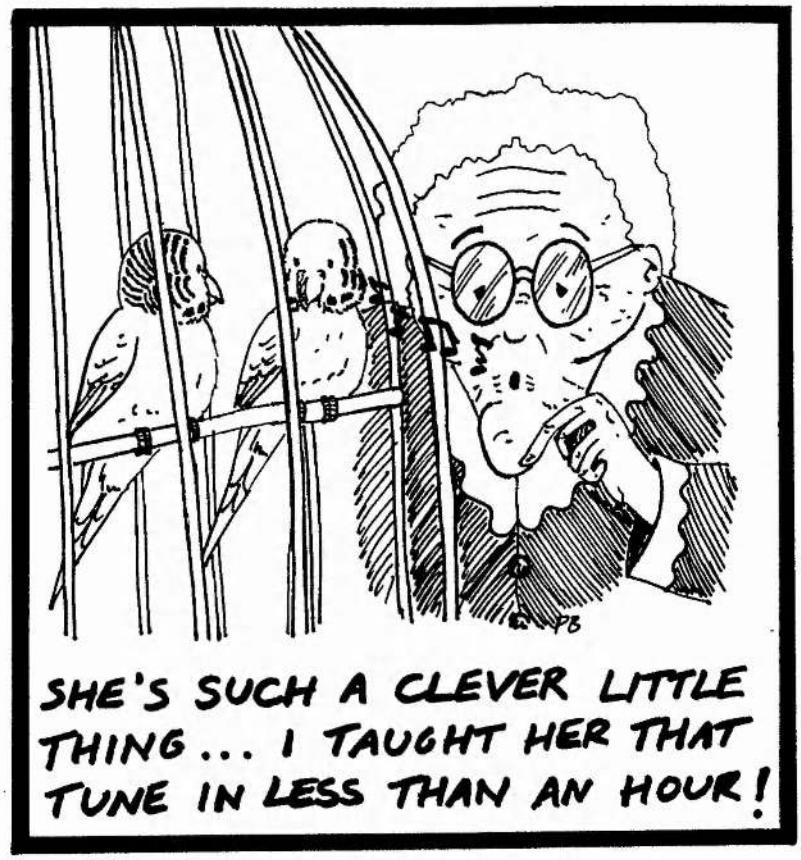
SHE'S SUCH A CLEVER LITTLE THING... I TAUGHT HER THAT TUNE IN LESS THAN AN HOUR!

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I am grateful to my parents Marie and Bob for their genetic input, and finally my thanks go to Caterina for giving me good reason to occasionally elope to the Dolomites, and for still being a faithful companion despite my external appearance.

Declaration

I, Paul Bartlett, hereby certify that this thesis, which is approximately 43000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

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I was admitted as a research student in October 1993 and as a candidate for the degree of Ph.D. in October 1994; the higher study for which this is a record was carried out in the University of St. Andrews between 1993 and 1996.

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ABSTRACT

Chapter 1 provides an introduction to the thesis by discussing the relevant literature on vocal learning in songbirds and parrots, with particular reference to calls, and setting out the aims of the following chapters.

Chapter 2 concerned an investigation of the similarity in the distance calls within and between families of zebra finches, involving fostering young birds to non-related parents. Male offspring were most similar in their distance calls to their male siblings with which they were raised and the adult male which raised them, suggesting an environmental influence in the acquisition of the call. There was also an indication that the call may be, at least in part, inherited. Females were most similar to their mothers and female siblings, though not to the same extent as in males.

Chapter 3 examined whether male zebra finches could exhibit vocal plasticity in adulthood, by learning new calls from other conspecifics, and whether social deprivation during a young bird's development would accentuate this tendency. Adult zebra finches could not learn new calls from other similarly raised cagemates, even if these birds were reared under conditions of extreme social deprivation and were presented with an appropriate normally-raised adult male tutor.

Chapter 4 described a study which investigated whether adult male budgerigars housed in soundproof boxes, could learn new calls from a tape recording in the absence of any social stimuli. Learning from tapes was very limited with only one bird producing an accurate copy of the playback, emphasising the importance of an interactive social context in vocal learning.

Chapter 5 attempted to determine exactly which social factors were most influential in determining the extent of call matching between adult male budgerigars. Certain individuals did match more closely in their contact calls; close proximity appeared to promote call convergence between cagemates.

Chapter 6 examined the effect of adding an unfamiliar budgerigar to an established flock, on the group specific call. It was found that, contrary to expectation, mutual imitation by all flock mates did not occur as other studies have shown, and that 'new recruits' conformed to the shared group call.

Chapter 7 concluded the findings of the five experimental chapters, and discussed their significance with reference to previous studies, including ideas for further investigation.

CHAPTER 1

INTRODUCTION

1.1 General Introduction

This thesis describes a series of laboratory experiments that examined various aspects of call learning in adulthood in two very different species of birds: the zebra finch (*Taeniopygia guttata castanotis*) of the Passeriformes order, and the budgerigar (*Melopsittacus undulatus*) of the Psittaciformes order. Both these two species can undergo very different processes of vocal learning, but being only distantly related, the mechanisms almost certainly evolved independently. The functions of calls in the two species are probably very distinct too.

This chapter begins with an introduction to the literature on call learning, with specific reference to passerine and psittacine species, in order to clarify the basis on which the experimental chapters of this thesis were designed. Following from this, brief descriptions of the life histories, ecology and behaviours of the two species in the wild are given to place the results of this thesis in their natural context. Other relevant descriptions include the normal development of the distance call in young zebra finches, and that of the contact call in budgerigars. Finally, the aims of the thesis are outlined.

1.2 Call learning in song birds and parrots

Although song learning and geographical variation in song are well known in oscines (Mundinger, 1982), they are less well documented in non-passerines. Indeed, it was once thought that whereas song is acquired by imitation in songbirds, it has developed independent of learning in non-oscines (Konishi & Nottebohm, 1969).

There are at least four orders of birds in which vocal learning is known to occur (Nottebohm, 1972; Kroodsma, 1982): the Passeriformes (Kroodsma, 1982), Psittaciformes (Gramza, 1970; Rowley & Chapman, 1986), and the Apodiformes (Trochilidae, hummingbirds; Snow, 1974; Wiley, 1971; Skutch, 1972; Baptista & Schuchmann, 1990; Atwood *et al.,* 1991), and Piciformes (Rhamphastidae, toucanets; Wagner, 1944). However, most of the studies in avian vocal learning have concentrated on the songbirds, or oscine passerines, of which there are over 4000 species. In these species, song is restricted mainly to males and the occurrence of song and territoriality is seasonal.

Vocal learning is thought to have evolved independently in all four orders, and hence we may expect to find differences in the processes and functions of learning from studies of species within these orders.

Vocal learning is the norm in two of these taxonomic groups, songbirds and parrots. Although it was once thought that the neural circuitry and specialised nuclei involved in vocal learning were homologous in parrots and songbirds (Paton *et al.*, 1981; De Voogd, 1986), recent neuro-anatomical and neuro-chemical studies suggest that the similarities are superficial (Striedter, 1994; Ball, 1994). In comparison with songbirds, the vocal control nuclei of parrots are in a different anatomical position (Paton *et al.*, 1981), receive auditory input from a different auditory pathway (Brauth *et al.*, 1987, 1994; Striedter, 1994), and lack some of the steroid receptors that are abundant in the songbird vocal control nuclei (Ball, 1994). This lack of homology at the neurological level suggests that vocal learning has arisen independently in these two groups.

Oscines, parrots and hummingbirds have in common a syrinx which is controlled by internal, as well as external musculature. Gaunt (1983) suggested that, because of this shared trait, hummingbirds could be capable of song learning.

Learning could be considered a risky way to obtain species-specific vocalisations; a bird may not learn the 'correct' vocalisations. For example, galahs (*Cacatua roseicapillus*) naturally cross-fostered after nest robbing by Major Mitchell's cockatoos (*Cacatua leadbeateri*), learn the calls of their foster parents and associate with their foster species, to the exclusion of their own (Rowley & Chapman, 1986).

For vocal learning to have evolved, it must confer some specific advantage. One such advantage is that vocal learning provides a mechanism for individuals to share sounds with particular conspecifics (e.g. neighbours, kin, mates, flock, or territorial group) rather than any conspecific (i.e. species-specific vocal characteristics shared with all conspecifics). By sharing vocalisations with a subset of conspecifics, a bird's vocalisation can denote information on species, sex, individual, and group identity.

Of course, vocal learning encompasses both song and call learning; on the basis of structure, ontogeny, and function, bird sounds have historically been classified as either songs or calls (Thorpe, 1961). Though there is much debate over the appropriate definitions of the two types of vocalisations, song can briefly be described as long, sustained, complex utterances which only the male of the species usually produces (Nottebohm, 1972), whereas calls are briefer, simpler sounds which are common to both sexes (Catchpole & Slater, 1995). This is obviously a large generalisation and there is much variety between species in the context, function and sex differences of songs and calls.

For instance, the budgerigar (*Melopsittacus undulatus*) has a complex varied vocal repertoire which consists of distinct call types, as well as a rambling, warbling song, which is performed by both the male and female of the species in a variety of contexts (Brockway, 1964, 1965, 1969; Trillmich, 1976; Wyndham, 1980; Ferrell & Baptista, 1982). Parrot song lacks the stereotypy of oscine song; it is composed of syllables that

are variable in acoustic structure, has no stereotyped syllable order, and does not have a set song length.

The traditional distinction between songs that are complex learned vocalisations used in territory advertisement and mate attraction, and calls that are innate vocalisations, is now considered to be inaccurate and artificial. Many species that do not learn have songs (e.g. suboscines such as flycatchers; Kroodsma & Konishi, 1991). Some species, such as the Corvidae, use calls for territorial advertisement and song for intragroup communication; some species have songs that are simpler in structure than their calls (e.g. black-capped chickadee (*Parus atricapillus*; Ficken *et al.*, 1978)). Many species that do learn song also learn calls (Mundinger, 1970, 1979; Güttinger, 1974; Marler & Mundinger, 1975; Poulsen, 1959; Nowicki, 1989).

The main functions of song have been described as territorial defence (Armstrong, 1973; Krebs, 1977; Krebs *et al.*, 1978; Yasukawa & Searcy, 1985; Falls, 1987; McDonald, 1989; Kroodsma & Byers, 1991; Westcott, 1992), mate attraction (Catchpole, 1983, 1986; Catchpole *et al.*, 1986; Eriksson & Wallis, 1986; Gibson, 1989; McDonald, 1989; Mountjoy & Lemon, 1991; Wiley *et al.*, 1991; Bensch & Hasselguist, 1992), and stimulation of female breeding behaviour and physiology (Brockway, 1965; Hinde & Steele, 1976; Kroodsma, 1976; King & West, 1977; Searcy & Marler, 1981; Wright & Cuthill, 1992). Calls on the other hand, are used to, for example, maintain contact, beg, threaten or denote alarm (Brockway, 1969; Catchpole & Slater, 1995).

There are certain parallels between passerines and psittacines, in the processes and functions of vocal learning. Young budgerigars will, shortly after fledging, form crèches where they soon develop a learned shared contact call, which may act as a group 'membership badge' and help to coordinate the movements of the flock (Treisman, 1978). Similarly, some songbird species that form stable flocks for part of the year, for example, black-capped chickadees, also show evidence that their species-specific

contact calls are learnt and may be used for group recognition (Mundinger, 1970, 1979; Ficken *et al.,* 1978; Mammen & Nowicki, 1981; Nowicki, 1983, 1989). Social interactions play a large, and perhaps critical role in the learning of contact calls in budgerigars (Farabaugh *et al.,* 1994), and similarly they also influence song learning in songbirds (Baptista & Petrinovich, 1984, 1986) and are particularly important in species that continue to learn new songs as adults.

As well as similarities in the processes of vocal learning, there are also functional similarities too. For example, black-capped chickadees can learn new contact calls in adulthood, develop flock-specific calls and can discriminate their flockmates calls from those of individuals in other flocks (Mammen & Nowicki, 1981; Nowicki, 1983, 1989). In both songbird and parrot species, these contact calls appear to function in establishing and maintaining social bonds within the flock (Mundinger, 1970, 1979; Ficken *et, al.,* 1978; Mammen & Nowicki, 1981; Nowicki, 1983, 1989; Farabaugh *et al.,* 1994).

Generally the songs of passerines are used in territorial defence or mate attraction, but in some species, particular those living in complex social groups such as Australian magpies (Brown *et al.,* 1988, 1992; Farabaugh *et al.,* 1988), songs may be shared and function in group affiliation rather like the 'songs' of some parrot species. On the other hand, some parrots duet for the purposes of nest and mate defence, and are therefore similar to some territorial duetting species of passerines (Farabaugh, 1982).

The warbling song of budgerigars is produced by both sexes and is accompanied in mated pairs by various courtship behaviours, including beak touching, courtship feeding and copulation (Wyndham, 1980). It also plays an important part in bringing the female into full reproductive condition (Brockway, 1965, 1969).

Evidence that some calls are learned has been available for many years. Sick (1939) described dialects in the rain call of the chaffinch (*Fringilla coelebs*), and such geographic variation is thought to arise through vocal learning. The ontogeny and neurologic foundations of call and song learning are similar. Male zebra finches, both wild and domestic, preferentially learn their distance calls and song from their fathers (Zann, 1990). The neural control of learned calls and song is identical in zebra finches, and differs from the neural control of unlearned vocalisations (Simpson & Vicario, 1990). In budgerigars, lesions of vocal control nuclei disrupt both learned song and learned calls (Hall *et al.*, 1994; Brauth *et al.*, 1994).

Much of the earlier work on vocal learning concerned song learning. Although this thesis concentrates on aspects of call learning, there are certain parallels that exist between the processes in which both are acquired, so a mention of the relevant song learning literature is justifiable.

Early experiments showed the importance of learning from an appropriate tutor in song development, by hand-rearing young birds in complete acoustic isolation from other conspecifics, and comparing their songs with those of normally reared adults (Thorpe, 1958; Marler, 1970). Birds reared in this way usually produced very impoverished songs that did not resemble normal song.

Experiments that followed involved defeaning young birds at varying ages. It seemed that the earlier a bird was deafened, the more abnormal was its song (Nottebohm, 1968; Marler & Sherman, 1983), suggesting the importance of practice and auditory feedback in the learning of song (Konishi's 'auditory feedback model', 1965). Song learning is now generally described as having a memorisation phase, known as the 'sensitive phase' of learning, and a 'production phase' when the bird continuously practices and refines its song.

Vocal learning in parrots however, is not restricted to a sensitive phase in which song and calls are acquired; learning and production are not separated in time (Dooling *et, al.,* 1987b; Brown *et al.,* 1988; Farabaugh *et al.,* 1994). Instead new vocalisations can be learnt throughout the adult life of a parrot.

Although Mundinger (1970) had shown that the calls of some cardueline finches were learnt, it was originally assumed that calls were innate (Thorpe, 1961) because they could develop without external models in some species (Güttinger & Nicolai, 1973). The latter study was based on the foster rearing of 15 different species of estrildid finches, which produced normal conspecific calls despite the lack of an appropriate conspecific model. However, evidence of geographical variation in the calls within species had suggested that vocal learning may have evolved in a wide range of species, for example: Indian hill mynahs, *Gracula religiosa* (Bertram, 1970); orange-winged Amazon parrots, *Amazona amazonica,* (Nottebohm, 1972); zebra finches, *Taenopygia guttata,* (Zann, 1984). Generally, the species that do learn their calls are from the same two orders for which vocal learning is common: the Passeriformes and the Psittaciformes.

1.3 Call learning in the zebra finch

Price (1979) studied the developmental determinants of structure in the zebra finch song and concluded that the calls, which can be incorporated into the song, provide song with conservative guidelines because he assumed the calls to be little affected by the rearing experiences. It has since been shown that calls are not innate, and are prone to be influenced by their social environment early in the development of the young zebra finch (Immelmann, 1969, 1972; ten Cate, 1982; Zann, 1984, 1985; Brindley, 1988; Jones, 1994).

That calls are sometimes incorporated into song may suggest that they undergo similar processes in their acquisition. In a wild population, approximately 50 % of birds incorporate a distance call (DC) into their song (Zann, 1990).

Güttinger and Nicolai (1973) foster-reared 122 individuals from 15 species belonging to 7 genera, using Bengalese finches (*Lonchura striata*) as the foster parents. Their results showed that foster-reared young males tended to produce calls that resembled more their conspecific call which they had no experience of, and concluded that the calls of all estrildid finches were innate.

Contrary to the results of fostering experiments by Güttinger and Nicolai (1973), Zann (1985) found that zebra finch call development could be affected by rearing conditions. Zann cross-fostered wild-caught zebra finches to Bengalese finches until 40 or 60 days after hatching, and then reunited them with their normal raised siblings until day 100 when their calls were recorded. He assessed the similarity between DCs by measuring four parameters of the call. All of the foster-reared males gave DCs that were completely different from their fathers and normal reared siblings, and of these, 16% learnt the DC of their Bengalese finch foster mother or father. A further 60% of foster reared males gave a typically zebra finch male call, except that the noise element (only present in males' DCs) was absent. Of the normal reared males, 30% produced calls that were identical to the DC of their father. Zann also found that the between family variation for sons, for three of the four measured parameters, was significantly greater than within family variation. Whether the duration of parental contact for 40 or 60 days appeared to have no affect on the outcome of the call. Zann concluded from these results that certain characteristics of the DC were learnt in zebra finches during a sensitive phase that terminated prior to 40 days of age.

Another experiment to delineate the sensitive phase of learning was conducted by Brindley (1988). Young zebra finches were raised with their father to varying ages,

ranging from 6 to 70 days, after which the young were raised by their mother alone. Only those males that had experience of the father after 25 days were able to produce an accurate representation of a normal adult male's DC. In a further experiment Brindley (1988) manipulated the tutors that a young bird was exposed to and found that the father, heard prior to the sensitive phase for call learning, is preferred to a second tutor when both are presented during sensitivity.

More recently, Zann (1990) found evidence for a higher rate of transmission of call notes than song between generations of wild zebra finches. It was suggested that the DC of the male offspring is learnt from the father before 40 days, compared to the song which is learnt during a sensitive phase from 35 to 65 days (Eales, 1985). Where the call note is the same as a song call note Zann suggested that the former could be learnt during the first 40 days of life and later, during the sensitive phase for song learning, used to form the song call note.

These results suggest that calls and song have different sensitive phases early in the development of the young bird, and that the father, heard prior to this period, is the preferred model when a second tutor is presented during the sensitive phase.

In an earlier study, Zann (1984) examined the extent of variation in the structure within and between individuals, colonies, sexes, geographical localities and subspecies in free-living and wild-caught zebra finches. There were no significant differences between flocks, and apart from differences between sexes, each individual was found to have a distinct DC. As in black-capped chickadees (Nowicki, 1983), there is potential for the DC to be used in individual recognition. If call notes were learnt earlier than song, they may be more likely to be copied from the father and thus reflect kinship.

1.4 The zebra finch in the wild

The zebra finch (*Taeniopygia guttata castanotis*) (see Fig. 1.1), is an estrildid species that inhabits most of inland Australia, including grassland, scrubland and open savannah woodland. Their distribution is governed by the availability of water, and as a result is somewhat patchy (Immelmann, 1965).

The diet consists mainly of grass seeds, of which many varieties are eaten (Zann & Straw, 1984), occasionally supplemented with insects caught on the wing or whilst foraging on the ground (Immelmann, 1965).

Zebra finches are very gregarious and typically associate in breeding flocks of around 50 to 100 individuals. These flocks may amalgamate outside the breeding season, when water and food resources are more scarce, to form large temporary flocks of up to 1000 birds.

The timing of breeding is essentially determined by the availability of water, and by temperature. As a result, the length of the breeding season can vary greatly, and when conditions are favourable, several clutches can be reared in succession (Butterfield, 1970). This ability to raise multiple broods within a short period of time and as soon as conditions dictate, enable populations of the species to regenerate quickly after droughts, and no doubt contributes to its status as the most common of all the grass finches on the continent.

The ability to breed when conditions are favourable at any time of the year, is enabled by the constant gonadotrophic activity of the pituitary gland, synchronous moulting and breeding, and the short time required before juveniles are mature enough to breed themselves (Immelmann, 1965).

Figure 1.1 Two male zebra finches.

Figure 1.2 A pair of zebra finches. The female (left) lacks the distinctive orange cheek patch of the male (right). Other morphological differences which are not obvious from this figure are the chestnut flanks and black and white striping on the male's breast feathers.

Zebra finches breed and nest within their small flocks, and there is much social contact with other members of the group during feeding, drinking or bathing, and periods of rest and preening around the colony. Nests are built close to one another, particularly when the geography of the land dictates a shortage of appropriate bushes or trees, such as open grassland.

Pair bonds are established between mates (see Fig. 1.2) and are thought to be maintained for life, although monogamy within a social breeding system is probably unlikely (Birkhead & Møller, 1992). Indeed extra-pair copulations and egg dumping, have been observed to occur in the wild (Birkhead *et al.*, 1988); 10.9% of offspring were the result of intra-specific brood parasitism, whilst 2.4% of the clutches were the result of extra-pair paternity (Birkhead *et al.*, 1990).

Both parents share the construction of the nest, and this undoubtedly helps to speed up breeding by capitalising on good environmental conditions. Approximately three to seven eggs are laid. Incubation is also shared, and commences when about half the clutch has been laid; it lasts for 12-16 days.

The altricial young are initially blind and can only make very faint begging calls from their third day after hatching. Both parents feed the chicks in the nest and vocalise to them. By day 20, the chicks are fully feathered and ready to fledge. They continue to be fed on or near the nest and maintain close proximity to their parents, particularly when roosting at night. Sexual maturity is reached at about 70 days, by which time the young have developed their adult plumage.

1.5 The calls of the zebra finch

The zebra finch is a highly vocal species, both in the wild and in captivity. It has at least nine distinct calls (see Fig. 1.3) in addition to the song (Immelmann, 1965; Zann, 1990). Many of these calls display a complex structure in which the sound energy is concentrated in harmonics, the lowest of which is referred to as the fundamental frequency.

Zebra finches vocalise almost constantly throughout the day, but certain calls are uttered more frequently than others: the 'distance call', the 'tet' and the 'stack', which are commonly given on the move. Other less common calls include: 'kackles', 'arks' and 'whines' between breeding pairs; 'distress' calls during aggressive interactions; 'long tonal' calls as a prelude to distance calls in young chicks; and 'thuk' calls that warn of predators. As well as these single distinct calls, 'undirected song' is given at anytime of the year, whilst 'directed song' is produced by the male during breeding and courtship (Zann, 1990).

The DC is the most characteristic vocalisation of the zebra finch, and is mostly uttered by isolated birds. The DC is a sexually dimorphic call: a short, ringing 'tia' in males, but a more nasal and flatter 'tiaah' in females (see Fig. 1.4). Males also tend to call more frequently than females.

Despite the sexually dimorphic nature of the DC, the call type is identified and classified as the same call in males and females because of the context in which it is given, and the fact that both calls are derived from the long tonal call (LTC) of fledglings.

It appears to function as an identity call, a lost call and a flight call, and it is usually emitted in flight, during mild alarm, when greeting newcomers, during courtship, and

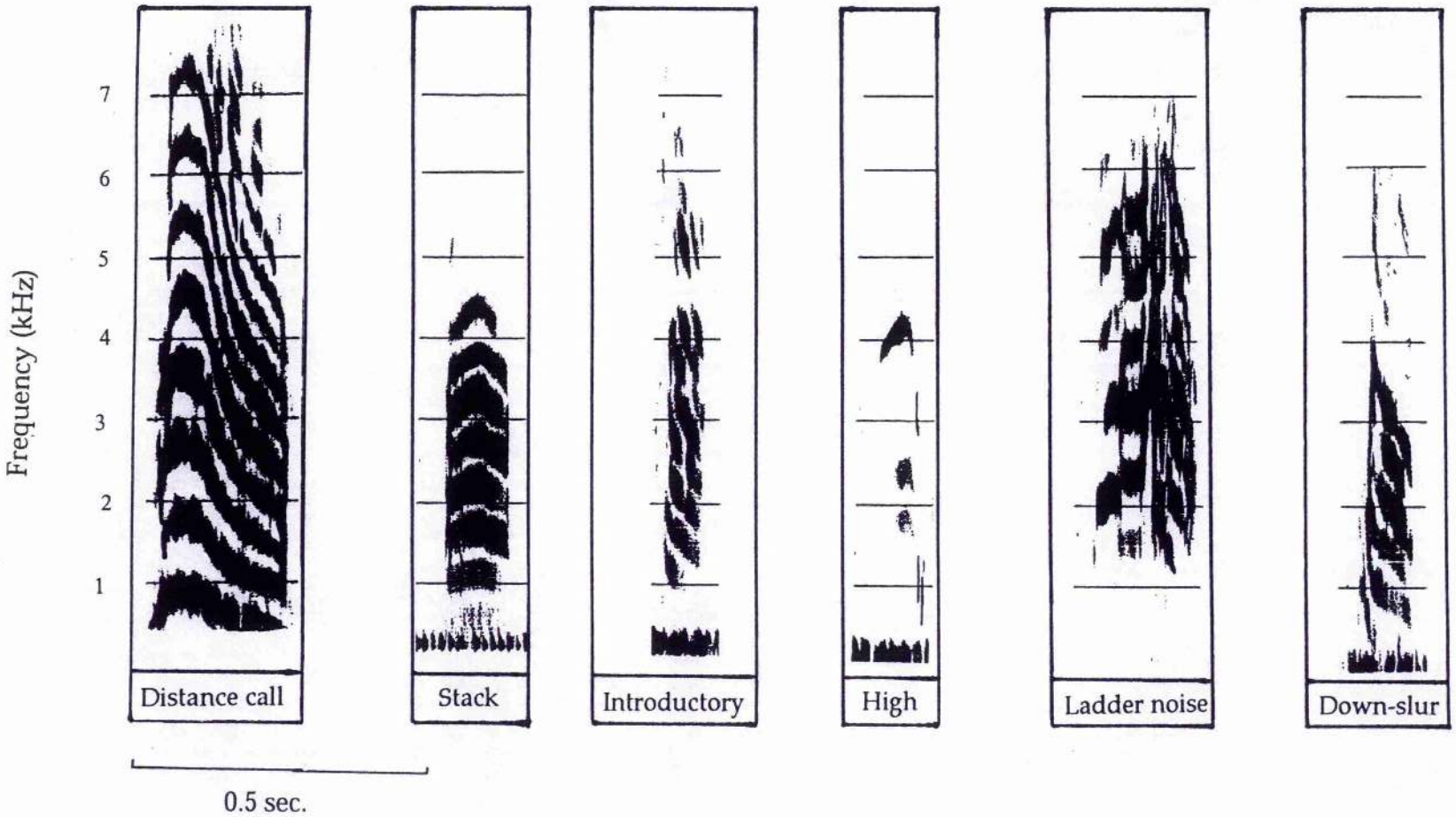


Figure 1.3 Sonagrams of some of the common call types given by zebra finches of both sexes (the distance call shown is a male type).

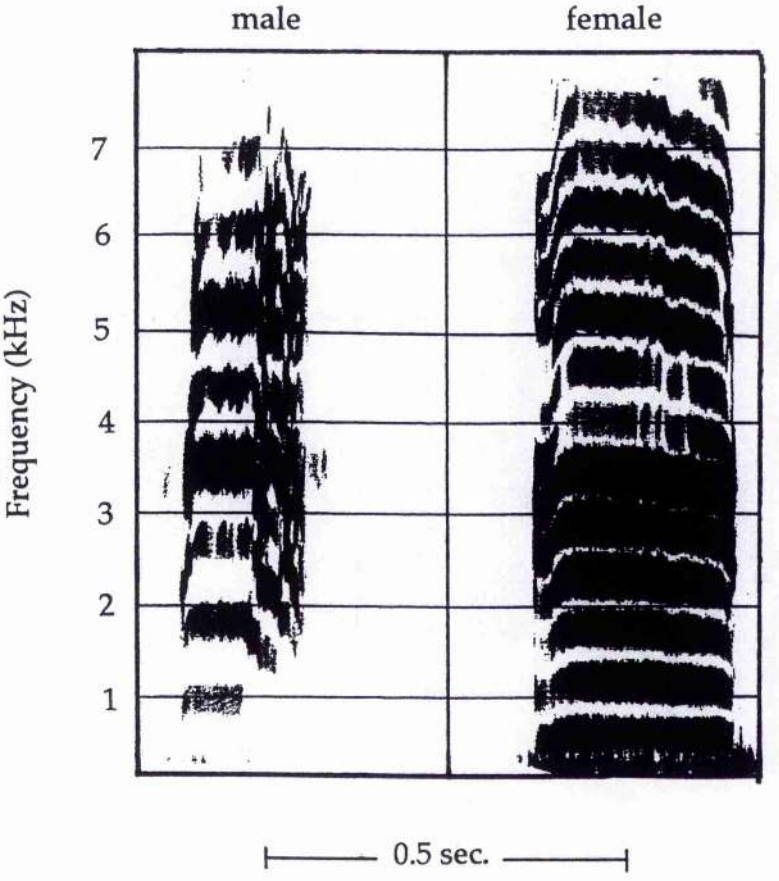


Figure 1.4 Sonagrams of the distance calls of male and female zebra finches. The main differences in the structure of the DC between the sexes are that it is shorter in males and females lack the noise element (the downslur at the end of the male call).

between bouts of feeding the young and singing. In the wild it is reported to be detectable at 80-100 metres away, and hence its use to locate separated flockmates. DCs have high reply rates, and may be exchanged between partners when one is at the nest and the other flying. When flocks mingle at feeding or watering sites, there is much use of the DC, probably to maintain contact with flockmates and the synchronicity of the flock's movements.

1.6 The ontogeny of the distance call in zebra finches

The development of the distance call in young zebra finches is a gradual process of change from the coarse repetitive begging calls that are uttered in the first weeks to the frequency modulated multiple harmonic structure of the adult bird by day 60-80 (see Fig. 1.5).

Within the first days post-hatching, young zebra finches produce their begging calls, which are initially soft and barely audible, but which become louder and more sustained in the following days. By day 15, some vocalisations are distinguishable from the harsh staccato of the begging calls, possessing a structure with strong harmonics and sounding purer. At this point, there is little of the frequency modulation that is evident in adult calls. Zann (1984) termed this call the 'long tonal call' (LTC), because of its long duration (0.2-0.4s), and they tend to occur during or close to begging calls. Indeed Zann reported that they were sometimes given in response to the DC of the parents. The use of LTCs to reply to the parents increased with age so that by day 20, parents and young were observed to answer one another on 80% of occasions (Zann, 1984).

The calls of both sexes originate from this LTC. By the time the young have fledged, at around day 22, the LTC has already started to change, it becomes shorter in duration and the harmonics more modulated and amplified. By day 35-40 the young birds have a

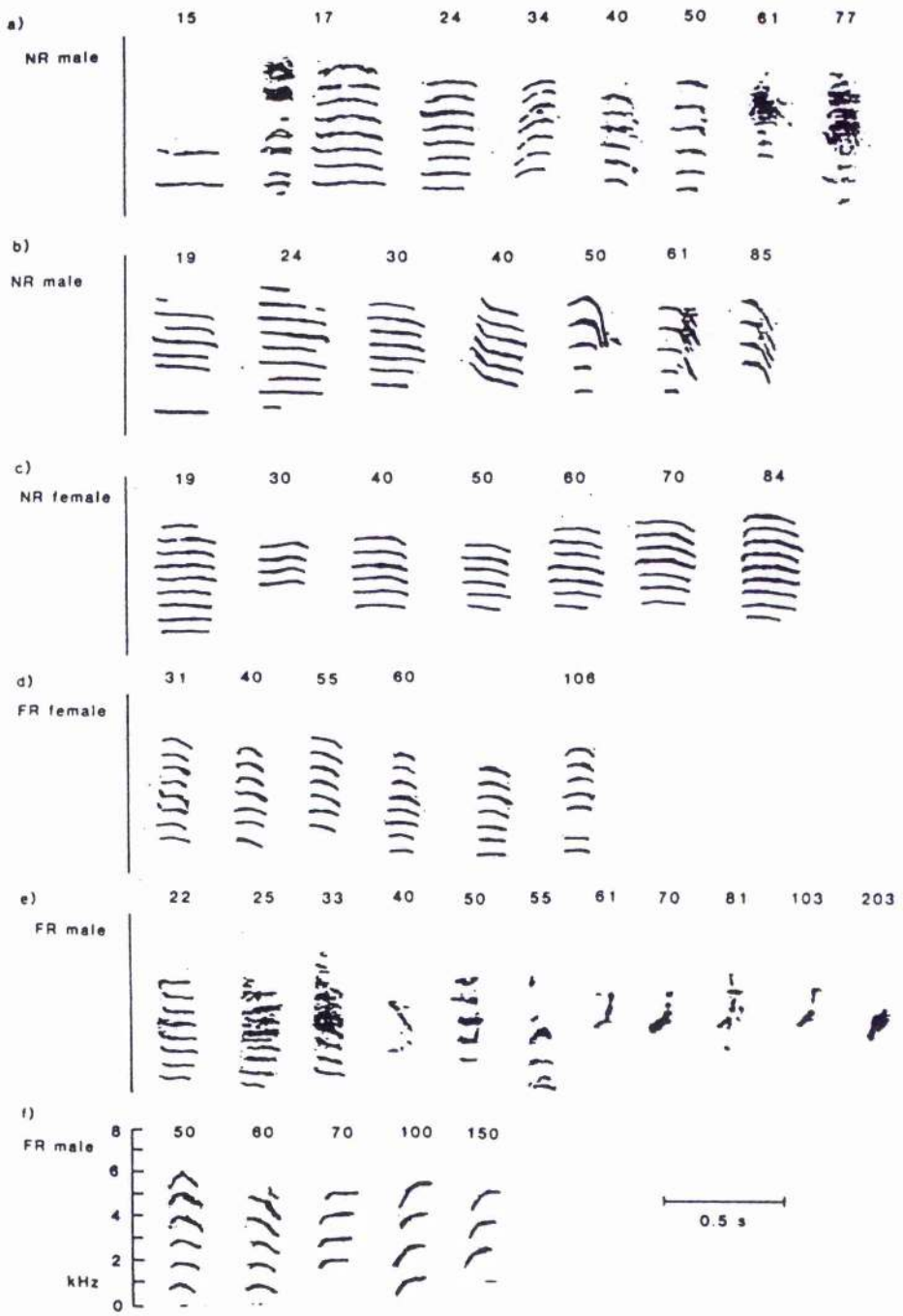


Figure 1.5 Changes in the structure of the distance call with age. a) Normal-reared male showing the prefledging long tonal call at day 15; at day 17 the call follows from a series of begging calls. b) Normal-reared male; c) normal-reared female; d) foster-reared female; e) foster-reared male which developed a male Bengalese finch DC; f) foster-reared male which developed the tonal male distance call. Numbers refer to days after hatching. (Taken from Zann, 1985).

call that is like that of the adult female DC. From this point females do not undergo any more alteration in their call, but males now begin to show rapid changes in frequency modulation.

At around day 40-50, the typical female type structure of the male DC becomes upslurred at the start and downslurred at the end, with an unmodulated middle section. By day 60, amplitude changes occur which result in the adult male DC, involving a disappearance of the initial upslur, the middle unmodulated section becoming the tonal element and the rapid downslur at the end becomes the noise element, which is the most sexually diagnostic feature of the male call. In addition, there is a reduction in the amplitude of the higher frequencies of the call, and particularly the noise element which is greatly reduced in all but the range of the frequency of maximum amplitude (FMA). The amplitude of the tonal element is more evenly spread among the harmonics. The fundamental frequency doubles from about 0.6 kHz to 1.2 kHz.

Females show no significant changes in the number and shape of the harmonics once they have achieved the stereotyped call by day 40. Males' DCs take about twice as long to mature as those of females, so that the complete adult male DC is not produced until the bird is between 70-80 days old, by which time the DC has developed two components and has become higher-pitched than that of the female DC. Variation in the rate of change of the DC is far greater in males than females.

It is not known why males should change their DC when it appears to serve the same function, and is, in the early stages of development, ontogenetically similar to the female's DC. It may be that it serves as a means of distinguishing sex when visual cues are obscured. DCs are also incorporated into the male's song, and may therefore function as a sexual stimulus to the female.

1.7 Vocal learning in the budgerigar

There has been much research into the processes of vocal learning in the passerines but comparatively little in the psittacines. Yet the parrots are among the species for which vocal learning has been most documented; indeed their potential for mimicry alone is widely known (Lorenz, 1970a; Todt, 1975; Nottebohm, 1976; Manabe *et al.*, 1995, 1997) and so acute that in some species, the imitation of non-conspecifics and even humans is possible in adulthood (Pepperberg, 1981, 1990a, 1990b; Pepperberg & Neapolitan, 1988).

Compared to the passerines, psittacines have received relatively little study. The species of psittacine that has been studied the most is the budgerigar; both field, and laboratory data have provided a good opportunity to compare vocal learning in psittacines with that in passerines. Yet it remains unclear how representative the budgerigar is as a species for comparing vocal learning and communication in parrots with those of songbirds. Some aspects of the budgerigar's vocal behaviour are indeed akin to the characteristics of parrots in general; a repertoire of functionally distinct calls, a learned contact call that has potential for use in flock and individual recognition, and the ability to learn new calls throughout adulthood. However, the large size of the call repertoire and the possession of a complex warble song are features that are not common to the order as a whole.

The functional significance of the large call repertoires of some parrot species has been the subject of debate (Farabaugh *et al.*, 1994). Brereton (1963) studied the complexity of vocalisations of Australian parrot species in relation to their social structure. His observations revealed that species that form small, stable flocks have larger call repertoires than those that tend to form larger amalgamations (e.g. the budgerigar), and concluded that this was because more information needed to be intimately exchanged between flock members in order to maintain the cohesion and stability of the group. In

budgerigars, for example, this would not be so important because of the relative unfamiliarity of many of the flocks members. However, Rowley and Chapman (1991) cautions that this study may be misleading in its assessment of repertoire complexity because of the subjective methods used in counting the number of calls (no sonagraph analysis was employed), and suggests the best approach would be a field study of social structure combined with a laboratory examination of the repertoire.

There have been many studies that showed the importance of social factors in the learning of song and calls in passerines (Mundinger, 1970, 1979; Baptista & Petrinovich, 1984, 1986; Slater *et al.,* 1988; Nowicki, 1989; Mann, 1991; Jones, 1994) and in psittacines (Pepperberg, 1981, 1990a ; Rowley & Chapman, 1986; Dooling *et al.,* 1987a; Pepperberg & Neopolitan, 1988; Farabaugh *et al.,* 1994). The budgerigar is a highly sociable bird that lives in close proximity with conspecifics in large flocks, and as such would provide an ideal subject for the study of the influence of social factors in vocal learning.

Farabaugh *et al.'s* (1994) study demonstrated the importance of social interactions in the learning of new contact calls in budgerigars. They housed budgerigars, each with a distinct repertoire of contact calls, in a cage and recorded the calls from each individual over an eight week period. Within a week there was already evidence of vocal learning between cagemates. Sharing began as imitation of another's call type but quickly developed into new call types composed of sections of call types from different birds. By the end of the eight weeks, all cagemates possessed the same group specific contact call. There was only very limited sharing of calls between groups that had been visually separated from each other within the same room. Thus, in the absence of social, but not aural contact, vocal learning was greatly reduced.

The shared contact calls of budgerigars can allow both individual and group recognition, like some other species which show similar imitative abilities. Black-

capped chickadees form wintering flocks with all individuals undergoing call convergence to produce a flock specific call (Mammen & Nowicki, 1981). Different chickadee flocks have distinctive calls, individuals can discriminate their own flockmates' calls from those of birds from other flocks (Nowicki, 1983). Thus, even though flockmates' calls are similar, some acoustic characteristics of chickadees' calls retain individual variability (Nowicki, 1989), and may allow individual recognition within the flock.

The budgerigar has been the subject of extensive psychoacoustic studies of basic hearing (Dooling & Saunders, 1975; Dooling & Searcy, 1981; Okanoya & Dooling, 1990). From tests of the birds' perception of complex vocalisations, it has been found that budgerigars have natural perceptual categories for calls drawn from their vocal repertoires (Dooling *et al.*, 1987). These categories are, to some extent, learned (Brown *et al.*, 1988), and there are sex differences in the perception of these calls (Dooling *et al.*, 1990).

Brown *et al.* (1988) used perceptual testing techniques to show that budgerigars could discriminate between different contact call types. Birds were then presented with four renditions of a shared contact call type by each of three birds that lived together. The perceptual abilities of the bird were so acute that the test subjects could even discriminate the individual versions of a shared contact call type, though not birds which did not have the shared call type in their repertoire.

Budgerigars clearly have the auditory abilities necessary for vocal recognition. They call more readily in response to their mate's call than to the calls of other budgerigars (Brockway, 1965). This ability to use shared contact calls for group and individual recognition may be advantageous in that it allows an individual living within a dense populous of conspecifics to not only locate the flock, but also mates within the flock.

1.8 The budgerigar in the wild

The budgerigar (*Melopsittacus undulatus*) is a small flock-living nomadic parakeet (see Fig. 1.6a and Fig. 1.6b) that inhabits the arid regions of central Australia (Rowley, 1974). The size of the flocks can be enormous, especially during droughts when combining flocks can form groups of up to several hundred individuals, and this is thought to be an adaptation to feeding on a widely dispersed but abundant food source such as grass seeds (Rowley & Chapman, 1991). Living in a large group increases an individual's ability to locate and exploit resources in a heterogeneous environment, and younger, less experienced birds can benefit from the local knowledge of older birds (Eastern and Pale-headed Rosellas; Cannon, 1984). Predator avoidance is probably another important function of living in a flock (Westcott & Cockburn, 1988). In these respects, the budgerigar is similar in certain aspects of its ecology to the zebra finch.

It is unknown whether the membership of flocks is stable, but in areas of low species density, small, cohesive flocks of 20-30 individuals do occur. However, mated pairs do generally tend to remain so from one breeding season to the next. This is thought to be advantageous for an opportunistic breeder, in order to take advantage of suitable breeding conditions as soon as they arise (like zebra finches, budgerigars are dependent on the availability of water to initiate breeding). Males actively court other females in the wild (Baltz & Clark, 1994), and in captivity (pers. observ.), and it is probable that extra-pair copulations do occur, though the frequency of extra-pair paternity is unknown.

Both sexes will excavate a suitable nest hole, incubate and rear the young (Wyndham, 1981). The male may also feed the female as well as the young (pers. observ.). Generally, four to nine eggs are laid at intervals of one day, with incubation starting immediately on the laying of the first egg. Incubation by both parents lasts for between

Figure 1.6a A domesticated male budgerigar

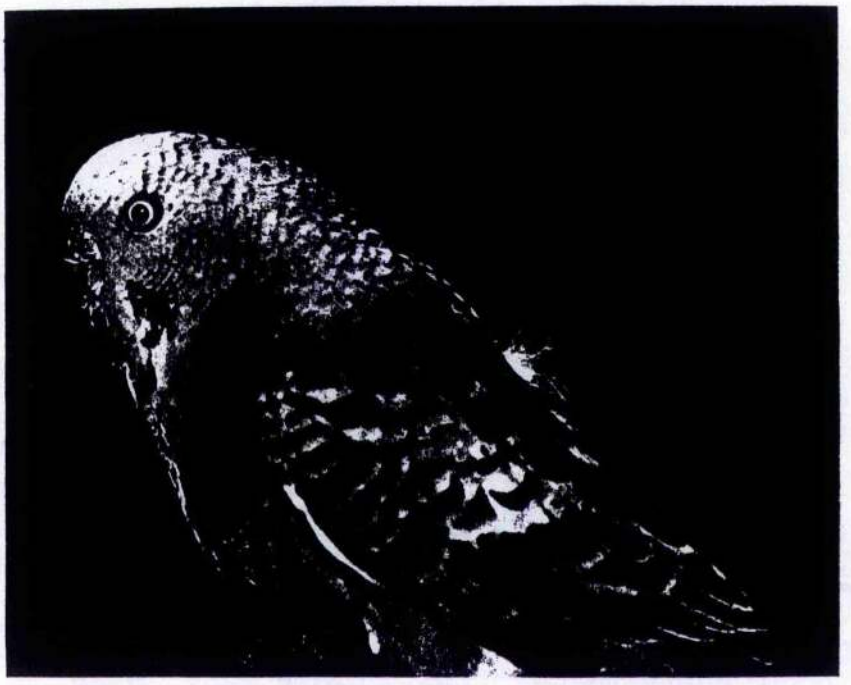


Figure 1.6b A domesticated female budgerigar

14 to 20 days. Hatching is asynchronous so that the oldest chicks are fledging well before their siblings leave the nest.

Fledging occurs at around 16 to 22 days of age, after which the young join a juvenile flock (Wyndham, 1980). Parents continue to feed their young at the crèche for about two weeks, with parents and young recognising each other's contact calls and flying towards each other (Brockway, 1964). After this time the young become independent and join juvenile flocks which leave the natal area (Wyndham, 1980). These flocks sometimes contain adults which have finished breeding.

1.9 The calls of the budgerigar

In adulthood, budgerigars have an elaborate learned vocal repertoire with which they coordinate social and reproductive behaviour (Brockway, 1964; Wyndham, 1980; Farabaugh *et al.*, 1992, 1994). The range of calls covers a number of acoustically and functionally distinct vocalisations. These include calls for contact, alarm, nest defence, courtship-feeding solicitation, agonistic harmonic chips and nestling food-begging calls (see Fig. 1.7).

The contact call is that which is used most frequently, and is given repeatedly when birds are in flight, separated from the flock, reunited with a mate, or when settling down to roost for the night. Individuals often have more than one contact call, and that which is most commonly uttered is known as the dominant contact call (Farabaugh *et al.*, 1994).

The contact calls of budgerigars are highly frequency modulated narrow-band vocalisations. They range between 2-4 kHz and last approximately 100-300 milliseconds. The pattern of frequency modulation can be extremely varied, even within

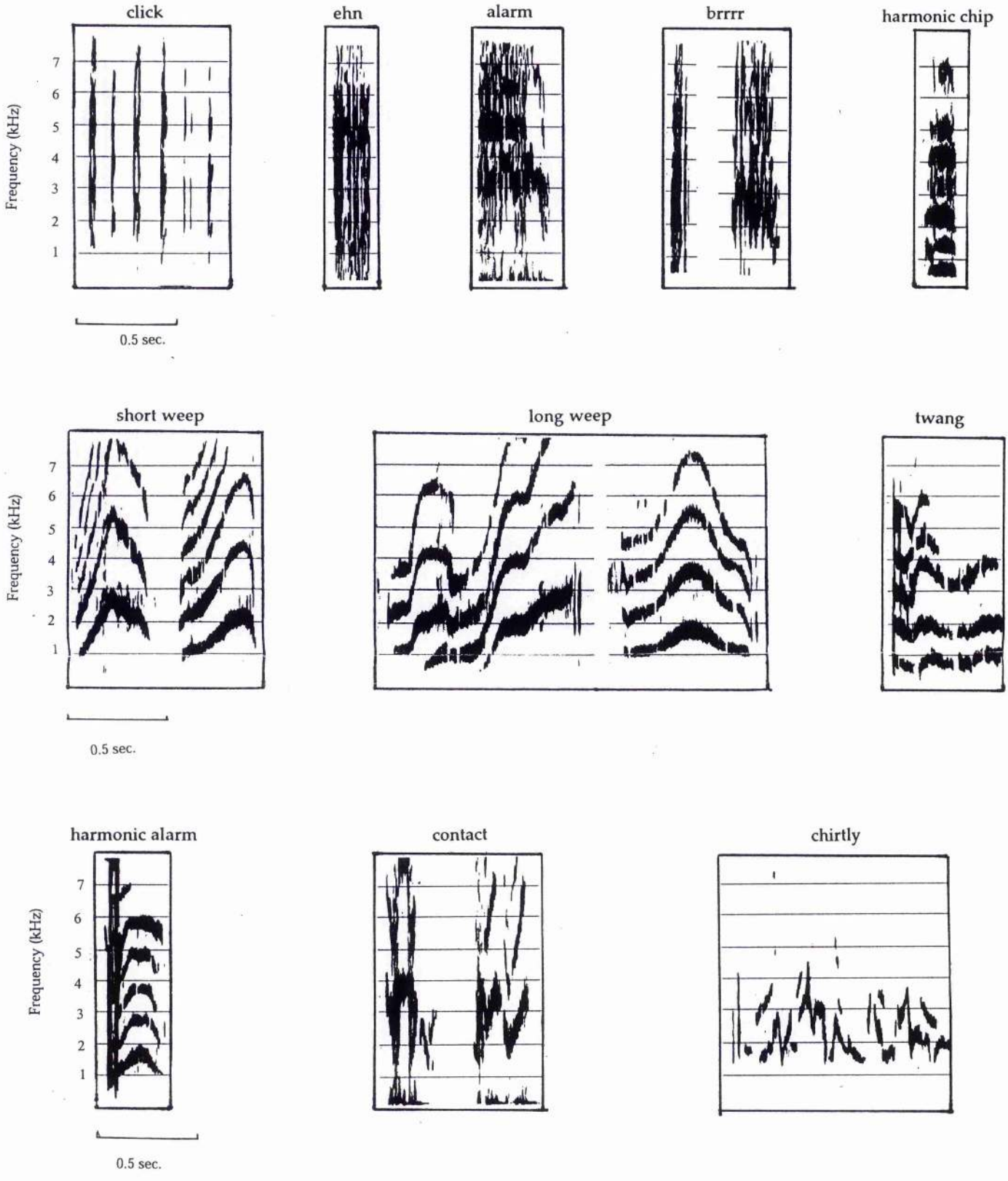


Figure 1.7 Examples of 11 acoustically and functionally distinct calls from a budgerigar's repertoire.

an individuals repertoire (see Fig. 1.8), yet the accuracy of repetitions of these calls remains high. Indeed, flockmates are able to develop a shared contact call, known as the flock-specific call, through mutual imitation of each others calls, known as call convergence.

At any given time, a budgerigar has a repertoire of one to several patterns, or contact call types; usually one or two types predominate, and account for 95-100% of all contact calls uttered (Farabaugh *et al.*, 1994).

The functional significance of learning contact calls from flockmates remains the subject of speculation, but it is thought to help budgerigars to locate, recognise, and maintain contact with mates and flockmates (Brockway, 1964; Wyndham, 1980; Pidgeon, 1981; Saunders, 1983), when flocks may intermingle at watering or feeding patches (Wyndham, 1980).

As well as a multitude of functionally distinct calls in the vocal repertoire of the budgerigar, there is also a long complex song composed of melodious warbling in which louder chirps and squawks are interjected, and which both sexes produce, though males at a much higher rate. Budgerigar warble song has no set length and varies greatly in structure, both within and among individuals (Farabaugh *et al.*, 1992). Many functionally distinct call types are embedded in the warble song, especially contact and alarm calls, but other syllable classes are found only in the warble song. Heterospecific mimicry is also incorporated into the song, for example mimicry of human speech in the warble song of domestic budgerigars (Gramza, 1970).

Warble song develops through learning; males in the same social group share a significantly greater proportion of their syllable repertoire with each other than with males in a different social group (Farabaugh *et al.*, 1992). Social interaction appears to guide what is learned, because a young male preferentially imitates the abnormal

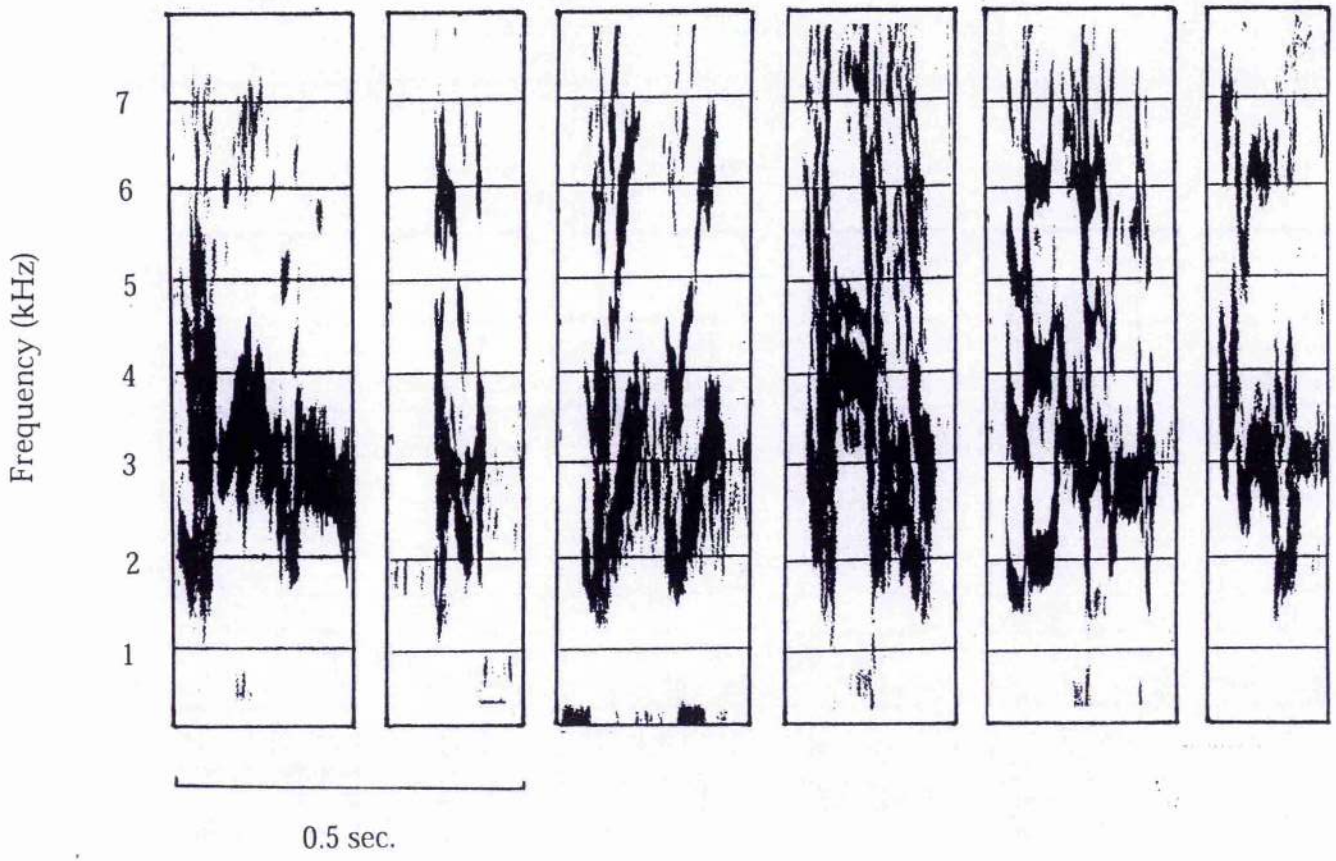


Figure 1.8 range of contact call types given by captive budgerigars.

syllables and temporal patterning of the warble of his isolate-reared cagemate, rather than the normal warble of birds in adjoining cages (Farabaugh *et al.*, 1992a).

The complex warble song is thought to have a role in the synchronisation of breeding between mates, since the species does not have a stable annual breeding cycle (Brockway, 1964, 1967, 1969). Budgerigars are capable of breeding several times a year if conditions are favourable, so they may not use external cues such as daylight to regulate their breeding. In these respects, the warble song may be an adaptation to stimulate gonadal development in non-seasonal breeders.

1.10 The development of the call in budgerigars

Young budgerigars start to produce begging calls about a week before fledging. These calls are individually recognisable from sonagrams, and it is conceivable that parents could theoretically recognise their young from them, though no experiments have shown this. Rowley (1980) did however, find that parent galahs (another Australia parrot species that is very similar to budgies in its ecology and social behaviour) could recognise their offspring from the last week in the nest. It is interesting that the acquisition of a distinctive call and possible parent recognition of this by parents, occurs just prior to the fledging of the young from the nest.

Although individually distinct, the calls do not resemble adult calls until a month after fledging. During this period they possess a stereotyped pattern of frequency modulation that is repeated a variable number of times (see Fig. 1.9).

Once they have achieved independence, young budgerigars already have a well developed vocal repertoire, including a range of contact and alarm calls and a long, complex warble song. At this time, budgerigars also begin to imitate their conspecifics'

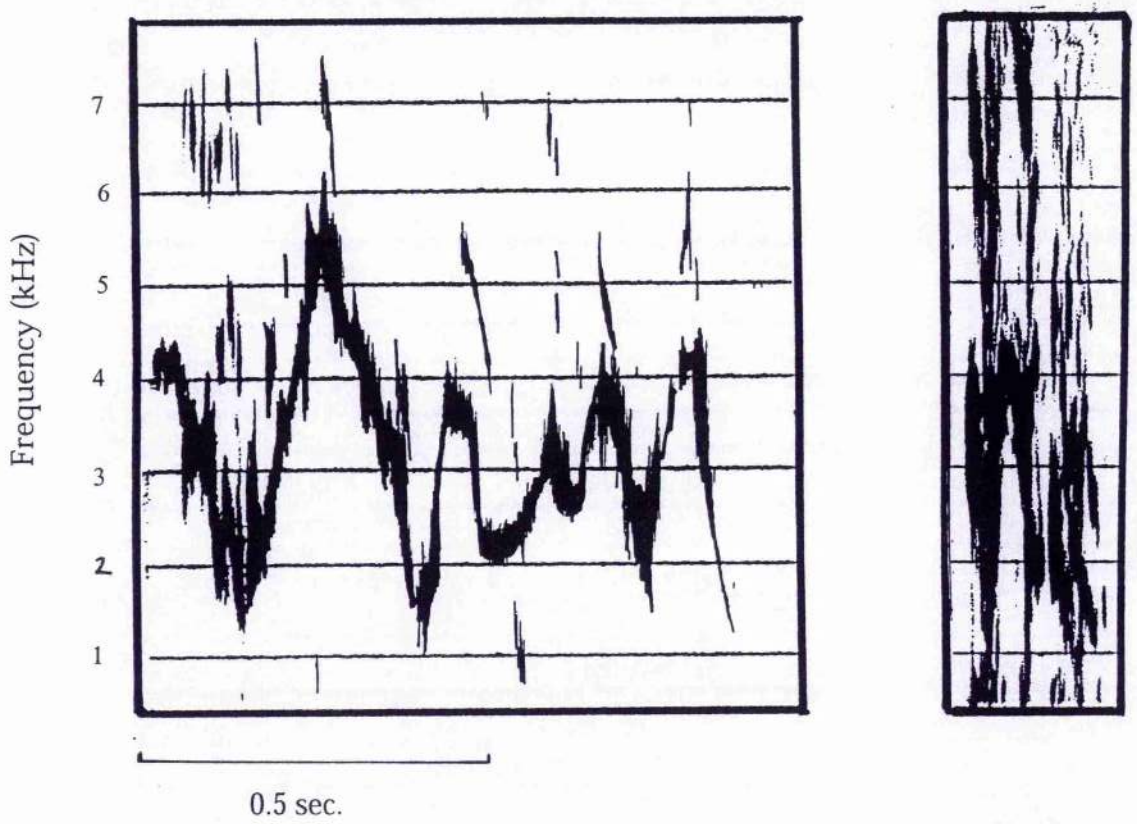


Figure 1.9 Sonagram of the stereotyped food-begging call (left) that precedes the production of an adult type contact call (right).

calls. Although they continue to do so throughout their adult lives, their ability to imitate appears to be greater at this stage.

1.11 The aims of the thesis

Chapter 2 describes a study which examined trends in the characteristics of the distance call between and within families of zebra finches. In other words whether the calls of closely related individuals were more similar than those between those of non-relatives. A previous study by Zann (1985) showed that the DCs of sons were almost identical to those of their fathers.

In addition, young chicks were fostered to other conspecific parents in order to determine if the trends observed were due to a genetic or environmental influence during the development of the chick post-hatching. Whereas Zann measured four specific parameters of the call, this study considered the shape of the call in its entirety and relied on cross-correlations to compare samples of the calls. This is a fairly new method in the analysis of avian vocalisations and therefore this chapter served as a test of the method of analysis which was employed in subsequent chapters.

In chapter 3 the potential vocal plasticity of zebra finches was investigated. As age-dependent learners, zebra finches had previously been thought to learn their vocalisations during a sensitive phase early in life, and for these vocalisations to remain stable throughout adulthood. Several studies have suggested that this may not necessarily be the case in passerines, and that under certain circumstances, new songs can be learnt after the sensitive phase (Eales, 1985; Baptista & Petrinovich, 1986; Jones *et al.,* in press). In this study, young male zebra finches were raised normally by both parents or under conditions of extreme social deprivation with only their mother. These males were then housed as adults with birds that had been similarly treated in order to

see whether the characteristics of their calls converged. It could therefore be determined whether there was evidence of vocal plasticity in normally-raised zebra finches, and whether there was more or less tendency depending on the social experiences of the bird during its development.

The affect that depriving birds of a social context in the learning of new vocalisations was also the subject of investigation in chapter 4. In this case, a different species was studied: the budgerigar, which is an age-independent learner and known for its extraordinary imitative ability of even non-conspecific vocalisations in adulthood. Farabaugh *et al.* (1994) had previously demonstrated call convergence between adult male budgerigars that had been housed together for a period of eight weeks. This chapter investigated whether budgerigars could exhibit call convergence to a tape recording instead of a live bird; in other words whether a social context was necessary for learning to occur. This was tested by isolating birds in sound attenuation chambers and playing a conspecific's contact calls through a speaker over an eight week period.

Chapter 5 examines the process of call convergence in budgerigars more closely in relation to the social context. Farabaugh *et al.'s* (1994) study concluded that call convergence in this species was achieved through mutual imitation because they were unable to determine whether some birds copied more than others. In this chapter, the experiment follows the protocol of Farabaugh by housing together birds with different contact calls and that had had no prior experience of one another, and tracing the process of call convergence. The use of cross-correlations allows the degree of similarity between the calls of individuals to be assessed. By making observations on the social behaviours of the subjects, it was possible to determine whether there was a relationship between certain social factors and how much and from whom an individual learnt.

Chapter 6 continues the study of call convergence in budgerigars, but attempts to determine whether certain individuals, by their status within the flock, are prone to copy more the calls of other group members. Previous captive studies on call convergence failed to simulate the social make-up of wild flocks by observing groups of birds where none of the individuals had had any previous experience of one another, which was contrary to the likely situation in the wild. In this experiment therefore, new recruits were introduced to established flocks of budgerigars, all of whom shared the same dominant contact call, and the calls traced over the 8 week period to see whether call convergence was mutual or biased towards the new bird or the familiar group members. This would help to ascertain the functional significance of call convergence in wild flocks of birds.

Chapter 7 summarises the findings and conclusions of the five experimental chapters in relation to each other and in the context of previous studies. Some discussion is made of the possible functional significance of the results to wild populations, and also of points of interest that would deserve further research.

CHAPTER 2

VARIATION IN THE DISTANCE CALL WITHIN AND BETWEEN FAMILIES IN THE ZEBRA FINCH

2.1 Introduction

Despite evidence from an early study that some cardueline finches learn their calls (Mundinger, 1970), calls were originally thought to be unlearnt in estrildid finches (Güttinger & Nicolai, 1973). This was based on a comparative study involving 15 different species of estrildids that were foster raised.

Price (1979) studied the developmental determinants of structure in zebra finch song and concluded that the calls, which can be incorporated into the song, provide the song with conservative guidelines because he assumed the calls to be little affected by the rearing experiences. It has since been shown that calls are more prone to be influenced by their social environment, particularly during a sensitive phase early in their development (Immelmann, 1969, 1972; ten Cate, 1982; Zann, 1984, 1985; Brindley, 1988; Jones, 1994).

It appears that young zebra finches are more likely to learn characteristics of their call during a particular period early in life, but it is still unclear whether the timing of the sensitive phase of call learning is prior to that of song learning in the zebra finch, and whether there is a degree of plasticity in the timing; in other words, can the sensitive phase of call learning be extended into adulthood if the conditions needed for normal vocal development are absent earlier in a zebra finch's life. Zann (1985) found that young birds that were exposed to parental contact for either 40 or 60 days, showed no difference in the similarity of their calls to the parent birds, indicating that the sensitive phase of learning for calls had occurred prior to 40 days of age.

Slater and Jones (1995) studied the timing of song and distance call learning by rearing young males with their fathers until 35 days and then caging them individually with a different adult male. They hypothesised that if distance call learning did occur earlier than that of song, there would be a tendency for young birds to learn the distance call of their father and the song of their tutor. There was no evidence from their results that the distance call was learned earlier and the song later; distance calls were not learned from the father to a greater extent than song, and therefore were no more likely to be used in kin recognition.

Brindley (1988) attempted to define the sensitive phase for call learning by raising young zebra finches with their father to varying ages, ranging from 6 to 70 days. After the father had been removed, the young were raised by the mother alone. In her experiment, it was only those male birds that had experience of the father bird after 25 days that produced an accurate representation of an normal adult male call.

In another experiment by Brindley (1988), young zebra finches were raised with their father until 35 days of age, and then provided with a second tutor as well as the father, both behind a wire mesh to control for tutor aggression. In this case there was a preference for learning call notes from the father.

Much of the work on call notes in zebra finches has been conducted by Zann. He carried out a study on the distance calls of free-living and recently captured zebra finches in order to establish the extent of variation in the structure within and between individuals, colonies, sexes, geographical localities and subspecies (Zann, 1984). He found that in male zebra finches, each bird had a unique distance call that was sufficiently distinct from others to provide a potential means of individual recognition. Inter-colonial comparisons revealed there to be no significant tendency for various

parameters of the distance call to differ between either neighbouring flocks or those from distant geographical localities.

A later study, also by Zann (1985), investigated genotypic and phenotypic influences on the ontogeny of the distance call, by comparing birds that were raised normally by both parents with young that had been cross-fostered to Bengalese finches. Of the cross-fostered males, 16% learnt the DC (distance call) of their Bengalese finch fosters, either that of their foster mother or foster father, and 60% gave a typically zebra finch male call, except the noise element (the most sexually diagnostic feature of the DC) was entirely absent. In contrast, some 30% of normally reared males gave DCs identical to those of their fathers and the remainder showed strong resemblance to them, so that the between family variation for sons was significantly greater than within family variation for three out of four parameters. From these results Zann concluded that the zebra finch male DC is at least partially learnt, and environmental input from the fathers' noise element is required to produce a normal adult male call.

From Zann's studies it is proposed that male zebra finches have individually distinctive distance calls and that certain similarities are evident within family groups. If this were the case, then there would be potential for individual recognition and kin recognition to occur.

The objectives of the present study were to investigate the similarity of the distance call within and between groups of captively bred zebra finches. In the present experiment, cross-correlation analysis was used which relies on the comparison of sonagrams of the calls as a whole along a time axis. The effectiveness of this technique in the analysis of animal acoustics has been shown by several studies (see below). By fostering young birds to unrelated pairs of zebra finches and comparing the DCs that they produce as adults, it may be possible to determine the extent to which learning can modify calls.

2.1.1 The development of SPCC in analysing animal acoustic behaviour

The earliest descriptions of bird songs were made using the musical scale and phonetic descriptions of sounds (Marler, 1952; Thorpe & Lade, 1961). These were obviously highly subjective (Jellis, 1977). It was not until the development of the sonagraph (Hinde, 1969) that the first visual representations of the time-frequency structure of sounds were possible. Sonagrams enabled accurate measurements to be made of the duration and frequencies of notes (Beecher, 1988).

While sound spectrograms have been the prominent tool in vocalisation studies (Borror and Reese, 1953), methods of analysing and comparing sounds had their limitations. Comparing sonagrams by-eye (Borror, 1965; Kroodsma, 1974; Mundinger, 1975) can often be a reliable method of analysing similarities between two call or song samples and tends to account for the sound in its entirety, yet the basis of categorisation is often unspecified and intuitive, and there is likely to be significant variation between observers. Another drawback with this assessment is that the quantification of similarities is not possible, and would in any case be rather insensitive to subtle differences in sound parameters.

Many avian vocalisation studies have limited their analyses to univariate statistical methods which are often incapable of identifying complex relationships among songs and calls. Another method which has commonly been used in sound comparison is that of measuring assigned parameters of the spectrogram, and employing multivariate statistics to analyse the frequency, amplitude, or temporal characters (Hjorth, 1970; Hopkins *et al.,* 1974; Johnson & Wichern, 1982;; Lemon *et al.*, 1981; Nelson, 1973; Slater, 1973; Zann, 1985). This technique does tend to quantify similarities, but could still be regarded as being fairly subjective since it is biased by the parameter choice of the observer.

Soucek & Vencil (1975) suggested using multivariate statistical methods to analyse note sequences within songs. Unlike univariate procedures, multivariate methods simultaneously use several independent variables to compare two or more groups. Because of this flexibility, multivariate techniques are preferable to univariate methods when comparing complex avian vocalisations. Sparling and Williams (1978) examined the potential of multivariate techniques for the analysis of bird vocalisations, but such techniques require the measurement of large numbers of variables and are thus highly laborious.

Methods were developed which would allow the objective comparison of vocalisations, accounting for the sound characteristics as a whole and therefore utilising all the available information. The basis for the sound comparative method is that a full representation of a sound's frequency-time structure, rather than just a few of its acoustic features, is more ideal for the analytical process. Although previous studies have used the whole of the sound (Miller, 1979; Goedeking, 1983), it was not employed, until relatively recently, in an automated process.

Digital spectrograms could be cross-correlated using the latest acoustic analysis software (Clark *et al.*, 1987). This technique has several main advantages; since individual parameters are not selected for, the observer can remain impartial and unbiased in obtaining a quantifiable measure of similarity.

Improvements in software capabilities of sound analysis programs have presented the acoustic biologist with an array of powerful tools with which to compare vocalisations. Spectrographic cross-correlation (SPCC) is potentially one of the most useful and applicable (McGregor and Ranft, 1994).

Clark *et al.* (1987) carried out a comparison between SPCC and multivariate analyses based on the song notes of the swamp sparrow (*Melospiza georgiana*). Their

comparison suggested that both methods were equally effective in analysis, the results being similar. Nowicki and Nelson (1990) carried out a similar comparison to Clark *et al.* (1987), and found no difference in the stringency of the SPCC and multivariate analysis in determining the similarity of sounds.

SPCC is now established as the most up-to-date method of acoustic analysis, with several recent studies employing the technique (Evans & Evans, 1994; Gaunt *et al.*, 1994; Lessells *et al.*, 1995; Nelson *et al.*, 1995). The main use of the technique in these studies has been to generate a single similarity measure (i.e. a peak correlation value (PCV)), which is then used as the data on which statistical tests are executed, such as ANOVA (Fotheringham & Ratcliffe, 1995) or cluster analysis (Gaunt *et al.*, 1994), as well as non-parametric significance tests (Mantel, 1967; Manley, 1991; Gaunt *et al.*, 1994).

The apparent ease with which these techniques can be employed with relatively little training could be considered a great advantage in the study of animal acoustic communication. However, some warn that due to this very accessibility, care should be exercised in ensuring that the method is executed correctly, with an appreciation of the shortcomings and potential pitfalls that can be encountered (Khanna *et al.*, 1997).

Khanna *et al.* (1997) conducted a series of tests that were designed to reveal the sensitivity of SPCC in comparing a variety of parameters; tests were designed to study the effect of varying a particular sound parameter on the SPCC. Sounds were artificially generated and duplicated to produce two samples that were identical. A single parameter was then altered in one of the copies, and compared by SPCC to the other duplicate. Parameters altered included varying the duration of notes, altering the frequencies and the frequency sweeps of notes, varying amplitude, and adding background noise. From their tests, they cautioned that SPCC must be used with care. Signals need to prepared correctly and noise should be filtered appropriately. Optimal

Fast Fourier Transfrom (FFT) lengths for calculating the spectrogram will depend on the length of the sounds being compared, differences in frequencies between the sound and slopes of FM sweeps.

Another limitation of SPCC is that it could only conceivably be applied to the note level; songs are simply too complex, involving variations in time interval between successive notes, different ordering of notes within the song and so on. If a song were to be analysed by SPCC, it would need to be dissected into its individual note constituents, and each note then analysed separately (a potentially lengthy and complex procedure). Gaunt *et al.* (1994) compared the songs of two hummingbird species, *Colibri coruscans* and *C. thalassinus*, but they elected to use only the first note of the song which was used similarly in all individuals. Notes which are rich in overtones are not suitable for SPCC analysis, particularly when the amplitude of overtones varies between notes (Wilkinson, 1994).

The problem of complex notes can, to a certain extent, be overcome by reducing the note to an appropriate unit (e.g. the fundamental frequency) by band-pass filtering, or using a spectral contour function. However, by doing so, the researcher is imposing the same sort of bias on the choice of parameters that previous methods employing measures of specific parameters of a sound were limited by, and the capabilities of SPCC therefore become relatively redundant. Also, certain species (e.g. Carolina chickadees, *Parus carolinensus*) can shift the dominant frequency between overtones and therefore notes from the same individual may vary (Khanna *et al.* 1997).

2.2. Methods

2.2.1. Subjects

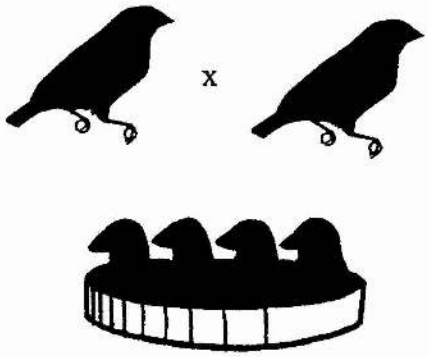
The subjects were zebra finches (*Taeniopygia guttata*) which had been captively bred in the laboratory. The birds were reared in breeding cages 80 x 60 x 30 cm in an animal house with a 14/10 light/dark cycle, an ambient temperature of 20/25° C and relative humidity of between 40-70%. All subjects were kept within the same breeding room so that birds could see and hear conspecifics in other cages and interact vocally with them.

2.2.2. Procedure

A total of 15 mated pairs of zebra finches were used for the experiment and their calls recorded prior to the commencement of breeding. They were then provided with nest cups and straw, and allowed to breed and raise their clutches under normal laboratory conditions. Interference was restricted to a daily routine of feeding and changing the water for the birds, and the room was hosed once a week. These pairs constituted the control group. The chicks hatched on day 14 of incubation and this day was termed day 1. Thereafter, they were recorded every five days to trace the development of the distance call (DC) in normally raised offspring.

A further 15 pairs of adult zebra finches were allowed to breed under similar conditions to the control pairs. After hatching, the clutch was split into two groups, and each of these two groups was then swapped for a similar number of chicks of approximately the same age from another pair's clutch. Therefore, each pair in the experimental group had a full clutch of unrelated chicks from two other pairs (see Fig. 2.1.1) (see also discussion for justification of fostering protocol). This procedure was performed when the chicks were between 5 and 13 days of age, after they had been rung for identification.

CONTROL GROUP: *Genetic parents and normally-reared offspring*



EXPERIMENTAL GROUP: *Foster parents and foster-reared offspring*

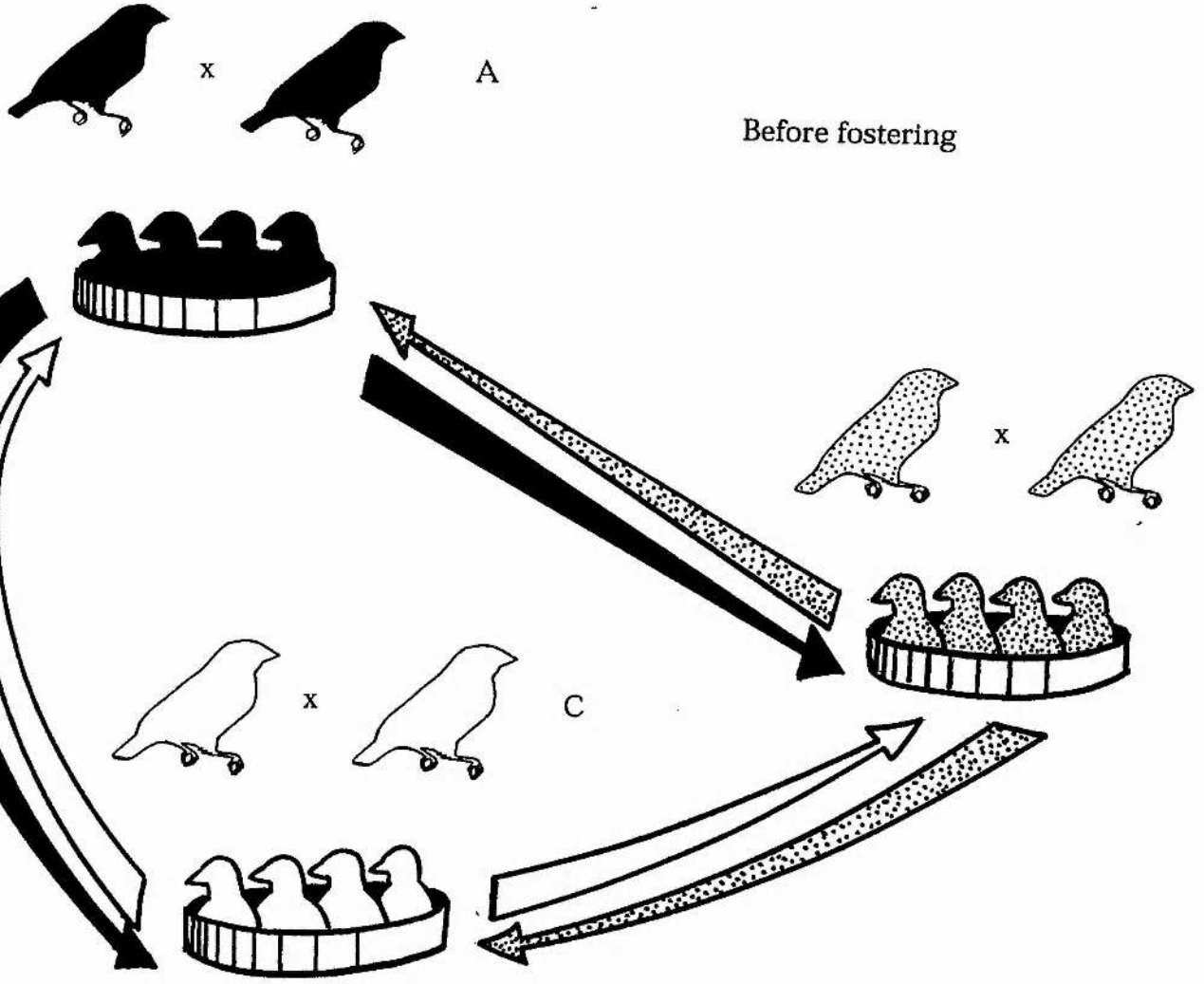
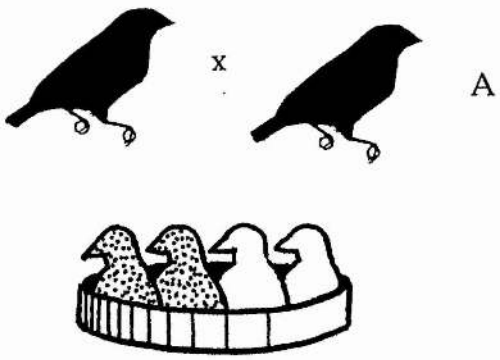
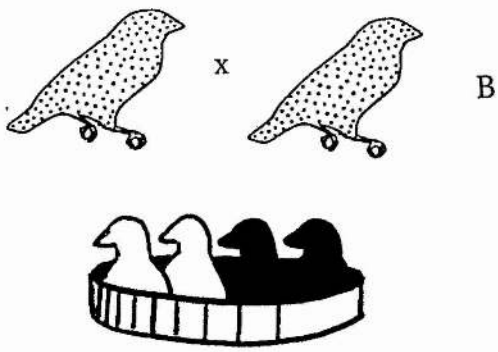


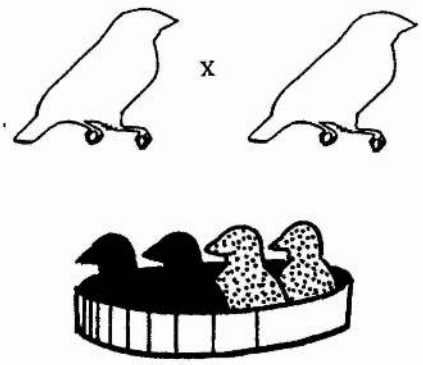
Fig 2.1.1 Control and experimental protocols illustrating the relatedness of family groups and the fostering process used

Control groups were allowed to raise their clutches of offspring with the minimum of disruption. All offspring were genetically related to both parents that raised them.

Experimental groups initially consisted of pairs of adults raising clutches that were their related offspring. However, after fostering, none of the young birds in each pairs' clutch were their genetic offspring. Therefore, for pair A, half the clutch were offspring from pair B, whilst the other half were offspring from pair C. This ensured that all offspring within experimental groups had been raised in a similar manner, thereby preventing the influence of nestmate interaction between young that had been foster-reared and those that had been reared under normal conditions.







The young zebra finches fledged from approximately day 19 to day 24 and were kept with their parents or foster parents until day 50. Following this period, all siblings from both control groups were removed and caged with their siblings in two separate rooms until day 100 when their distance calls were recorded. During this time each sibling group could see and hear the other similarly treated groups in neighbouring cages (individual isolation could not be achieved due to space limitations).

2.2.3. Recording and analysis of distance calls

The offspring were recorded on day 100 when each individual was removed from its sibling group cage and placed in a sound attenuation chamber (see Fig. 2.2) in a separate room. The sound attenuation chamber was fitted with a Sennheiser MD 400 microphone (frequency response of 300-15 000 Hz + 6db) leading to a Marantz CP 430 recorder which was set at the 0dB level with a recording volume of 8. The microphone was located 15cm away from the perch on which the subject was placed within the confines of an inner chamber measuring 30 x 40 x 30 cm.

A sample of approximately 20 DCs were recorded, but no fewer than 10. The DC was defined operationally by Zann (1985) as the loudest, longest type of vocalisation emitted by a zebra finch when it was visually isolated from its parents and siblings. In some cases individuals were played conspecific calls from a Marantz recorder and through a Sony SRS-A20 2 Watt speaker which was fitted inside the sound attenuation chamber. If this did not suffice to evoke a calling response, the birds were further disturbed by switching the light inside the chamber on and off several times, and this operation usually resulted in the bird being sufficiently alarmed to produce a sequence of rapid distance calls.

The calls were firstly analysed by eye on a Kay DSP Digital Sonagraph model 5500. Sonagrams of each individual's sample of calls were examined and any calls that were not DCs were disregarded. Measurement of the similarity between calls were made

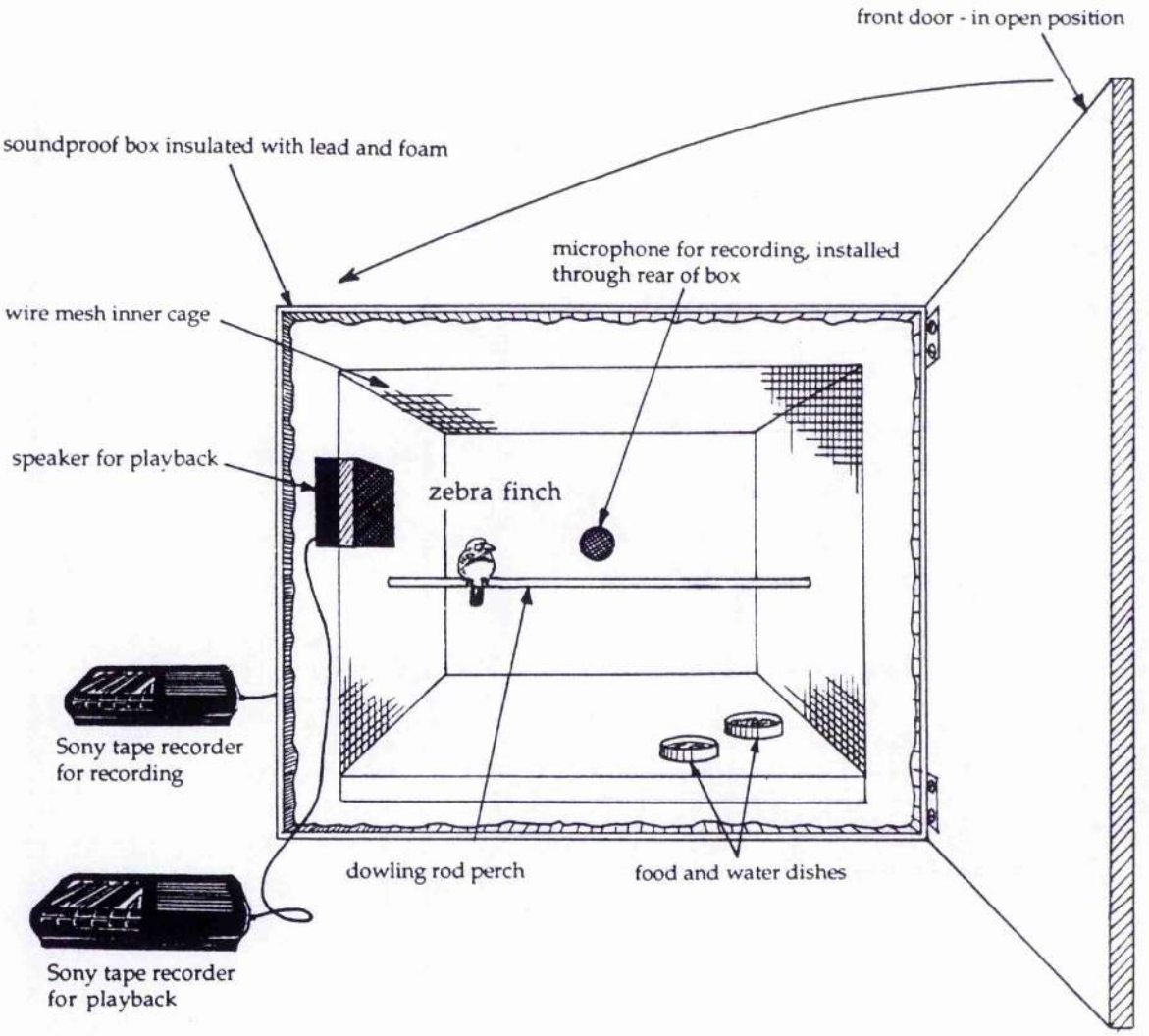


Figure 2.2 Soundproof box in which zebra finches were recorded.

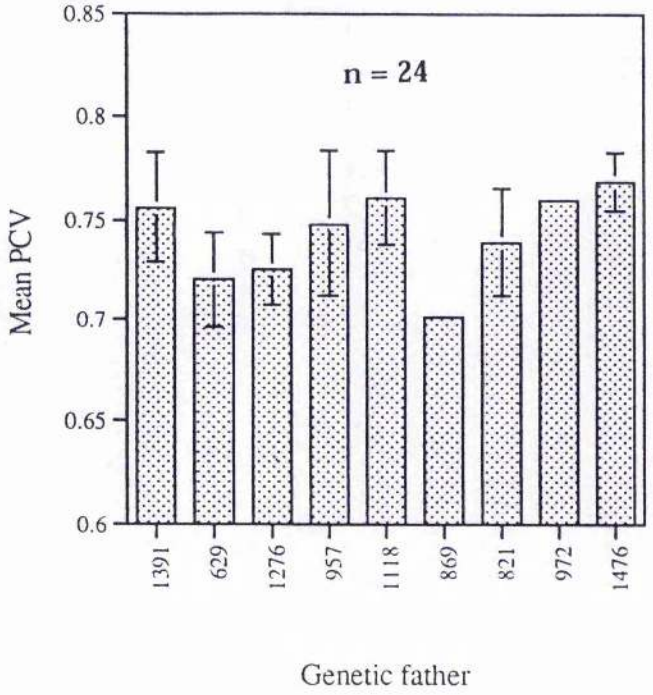
using comparisons of the shape of calls as a whole. A method known as cross-correlation analysis was employed which measures the extent of the maximum shared overlap between two digitised sonagrams as they are passed through a time domain (see Appendix A.2.1). Cross-correlations were performed using Engineering Design's SIGNAL (version 3.0) software (a Hanning window was used with a sampling rate of 20 kHz; upper frequency limit of 8 kHz; Fast Fourier Transform (FFT) size of 512; FFT interval of 13.2 msec; frequency resolution of 39.1 Hz; and a time resolution of 25.6msec).

2.3. Results

Cross-correlations were performed between the distance calls of male offspring and their genetic fathers and foster fathers in the experimental group, and genetic fathers and sons in the control group. The degree of similarity between fathers and sons is expressed in terms of the peak correlation value (PCV) which represents the maximum correlation obtained from comparisons of the two sonagrams.

2.3.1. PCV comparisons between fathers and sons

Fig. 2.1. and 2.2. show the mean PCVs between fathers' and sons' distance calls from the control group and the experimental group. The mean PCV for each family (denoted by the identity of the male parent) is derived from an average of the PCVs of all genetic siblings with their genetic or foster father within a family (standard deviation bars are shown). The mean PCV therefore represents the average value for each family. From Figs 2.1. and 2.2. the PCVs between genetic fathers and their sons in the control group (Fig. 2.1.1) appear to be slightly higher (mean = 0.741) than those between male offspring and their foster fathers (mean = 0.724) which have higher PCVs than fostered sons and their genetic fathers (mean = 0.705) (fig. 2.2.).



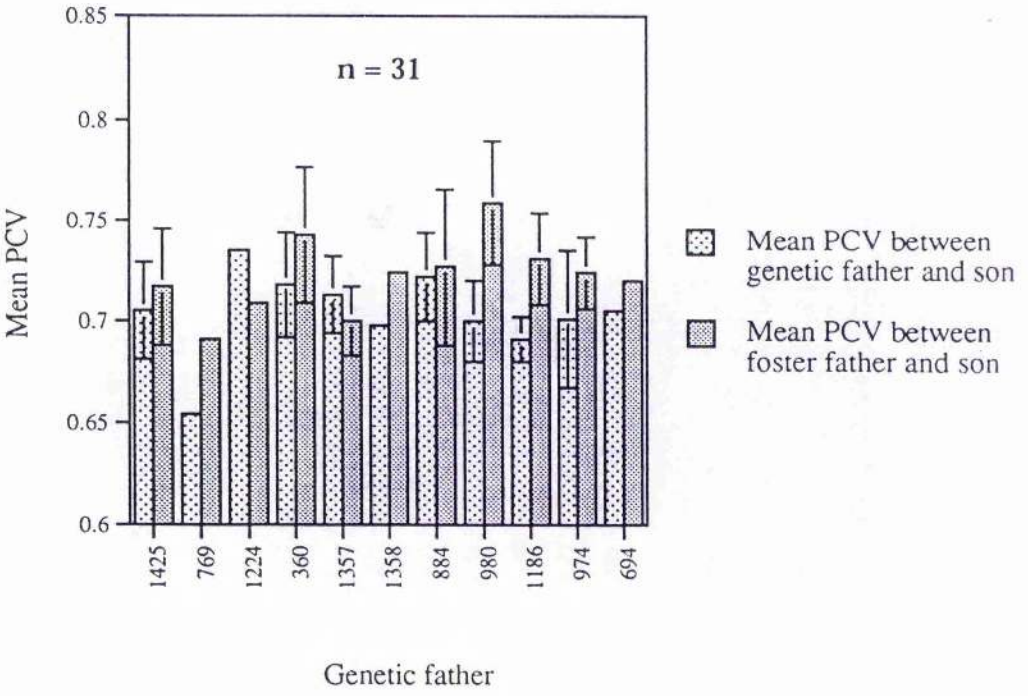


Fig. 2.1. & 2.2. Mean PCVs between fathers and sons in normally reared (top) and foster reared (bottom) groups. The mean PCV is derived from the PCVs of fathers and each male offspring (standard deviation bars are shown).

Table 2.1. shows the results of bootstrap comparisons between various combinations of groups of different relatedness, including sons and daughters, genetic and foster parents, and mothers and fathers. However, there is difficulty in determining what a suitable alpha level should be. Setting it at 5% means that there will be a greatly increased chance of significance where it doesn't exist. Therefore, to account for the multiple comparisons, in this case six different combinations of foster/genetic parent-offspring comparisons, reducing the alpha level will reduce the chances of a Type I error occurring, and the results will be more stringent. In this case it has been set at $P<0.008$ (i.e. 0.05/6), ensuring that any z-scores above 2.8 would be significant.

The z-scores indicate that there is a significant difference between the PCVs of genetic fathers and sons in the control group, and the PCVs of genetic fathers and sons in the group where offspring were fostered ($z = 3.50$, $P<0.008$ from 500 bootstraps). Although we cannot conclude with any degree of certainty that all other comparisons with z-scores between 1.96 and 2.8 are significantly different from one another (since our stringent alpha level is set at $P<0.008$), these results are nevertheless interesting. The PCVs of fathers and sons in the normally-raised (NR) control group are significantly higher at the $P<0.05$ than those between sons and their foster fathers in the experimental group ($z = 2.10$, $P<0.05$, from 500 bootstraps). Sons and their genetic fathers in the foster-raised (FR) group also had lower PCVs than those young males had with their foster fathers ($z = 2.32$, $P<0.05$, from 500 bootstraps).

The greatest extent of matching of the distance call between offspring and their adult male parent, was observed between young birds and the males that raised them. If this male was also the genetic father, it appears that significantly more of the characteristics of his call were learnt.

Bootstrap group comparison	z-score	Significance
FR genetic mother & FR foster mother	1.03	P>0.05
FR genetic father & FR foster father	**2.32**	**P<0.05**
FR genetic mother & NR genetic mother	0.46	P>0.05
FR foster mother & NR genetic mother	1.19	P>0.05
FR genetic father & NR genetic father	**3.50**	**P<0.01**
FR foster father & NR genetic father	**2.10**	**P<0.05**

Table 2.1 Z-score results from 500 bootstrap comparisons between the mean PCVs of male offspring and parents of varying relatedness and sex. PCVs between offspring and parents were initially obtained by cross-correlation of the distance calls. Z-scores above or equal to 1.96, 2.58 and 2.8 indicate significance difference between groups in the similarity of calls of parents and the young males they raised at the 5%, 1%, and 0.8% alpha levels respectively.

Bootstrap group comparison	z-score	Significance
FR genetic mother & FR foster mother	**1.96**	**P=0.05**
FR genetic father & FR foster father	1.18	P>0.05
FR genetic mother & NR genetic mother	**2.82**	**P<0.01**
FR foster mother & NR genetic mother	0.96	P>0.05
FR genetic father & NR genetic father	**2.04**	**P<0.05**
FR foster father & NR genetic father	1.59	P>0.05

Table 2.2 Z-score results from 500 bootstrap comparisons between the mean PCVs of female offspring and parents of varying relatedness and sex.

2.3.2. PCV comparisons between mothers and sons

Figures 2.3. and 2.4. show the PCVs of sons and mothers in both groups. According to these figures the PCVs of cross correlations between the distance calls of sons and mothers appear to be more variable between families and lower than those of fathers and sons. Indeed a bootstrap comparison between the PCVs of male offspring and their mothers and fathers indicated that the DCs of young males were more like their fathers' than their mothers'; comparison between the PCVs of sons and genetic mothers and sons and genetic fathers from the FR group ($z = 3.43$, $P<0.008$, 500 bootstraps), between the PCVs of sons and foster mothers and sons and foster fathers ($z = 2.84$, $P<0.008$, 500 bootstraps), resulted in significant z-scores which indicated that sons are more similar in the details of their distance calls to their fathers than they are to their mothers. The comparisons between the PCVs of sons and their genetic mothers and genetic fathers in NR group ($z = 2.05$, $P<0.05$, 500 bootstraps) were not significant at the 0.008 level, but were significant at the 0.05 level.

There was no affect of rearing conditions on the PCVs of mothers and sons. All mother and son cross-correlations resulted in PCVs that did not differ significantly between NR sons and genetic mothers, and FR sons and genetic mothers and foster mothers, suggesting minimal inheritance or learning of distance calls between mothers and sons.

2.3.3. PCV comparisons between fathers and daughters

The PCVs of cross-correlations between fathers and daughters, appeared to resemble more those of mothers and sons and were lower than those of father and son comparisons. This highlights the sexually dimorphic nature of the distance call.

Figures 2.5. and 2.6. represent the PCVs of FR and NR fathers and daughters and the results of bootstrap analysis of these groups are shown in Table 2.2. None of these comparisons were significant at the 0.8% level, although a significant difference existed

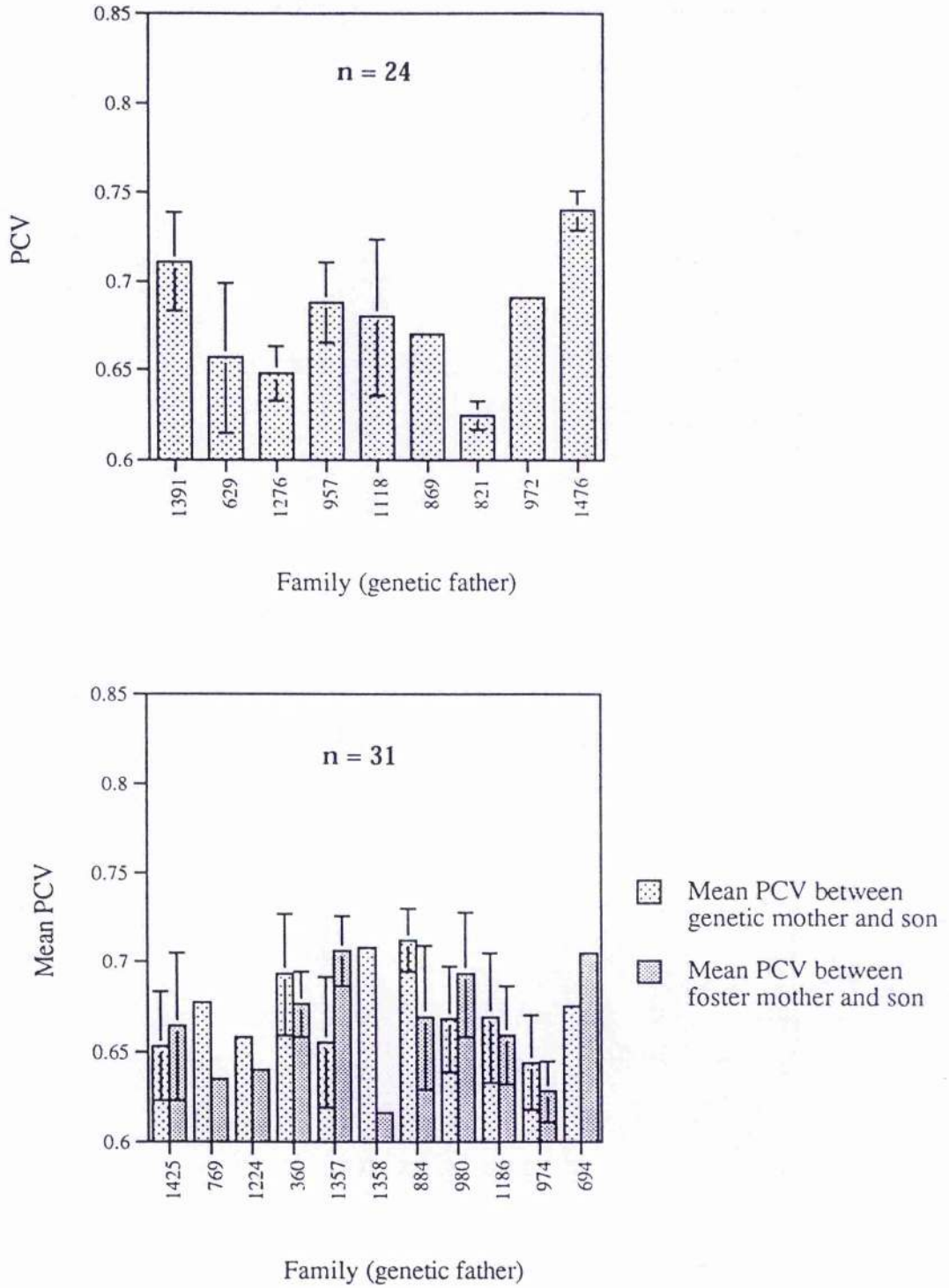


Fig. 2.3. & 2.4. Mean PCVs between mothers and sons in normally reared (top) and foster reared (bottom) groups. The mean PCV is derived from the PCVs of mothers and each male offspring (standard deviation bars are shown).

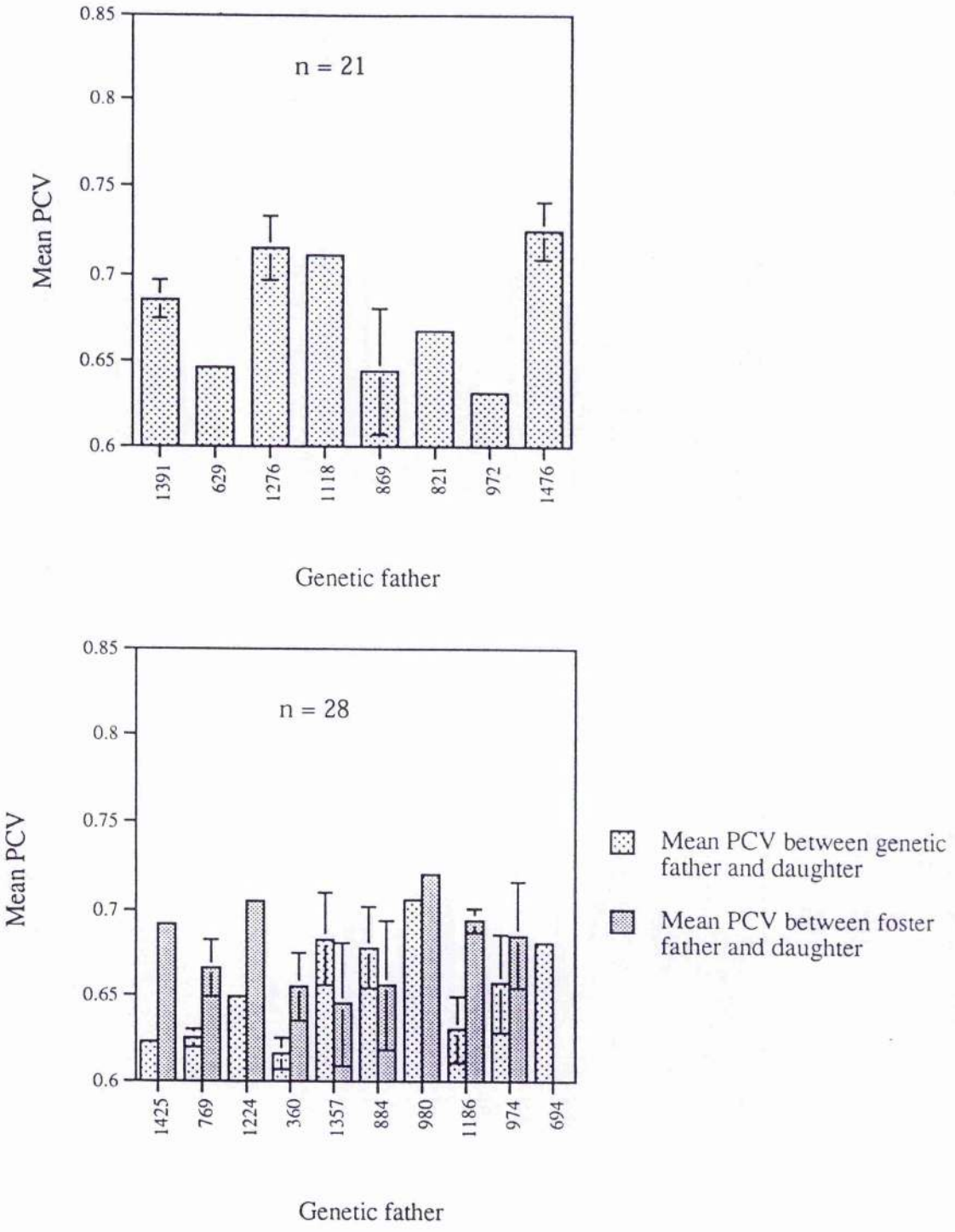


Fig. 2.5. & 2.6. Mean PCVs between fathers and daughters in normally reared (top) and foster reared (bottom) groups. The mean PCV is derived from the PCVs of fathers and each female offspring (standard deviation bars are shown).

at the 5% level in the PCVs of NR genetic fathers and daughters and FR genetic fathers and daughters ($z = 2.04$, $P<0.05$, 500 bootstraps).

The results of cross-correlations between fathers and daughters were compared with those of mothers and sons by bootstrap analysis, e.g. FR genetic father and daughter PCVs were compared with FR genetic mother and son PCVs. There were no significant differences between any of the three treatment group comparisons.

2.3.4. PCV comparisons between mothers and daughters

Figures 2.7. and 2.8. show the PCVs of cross-correlations between mothers and daughters. Although the PCVs are not as high as those between fathers and sons, they do nevertheless indicate that there is much in common in the calls of related females.

Genetic mothers in the NR group, and foster mothers in the FR group were equally similar in their calls to the female offspring that they had raised ($z = 0.96$, $P>0.05$, 500 bootstraps). Genetic mothers and daughters in the FR group had PCVs that were significantly lower than all other comparisons ($z = 2.82$, $P<0.008$, 500 bootstraps, for genetic mothers and FR daughters with genetic mothers and NR daughters; $z = 1.96$, $P=0.05$, 500 bootstraps, for genetic mothers and FR daughters with foster mothers and FR daughters). This perhaps suggests that learning has an influence on the distance call in female zebra finches.

2.3.5. PCV comparisons between siblings

There were no significant effects of having been normally raised or foster raised on the similarity between male siblings' DCs and those of female siblings. Figure 2.9. shows the mean PCVs of NR and FR brothers and NR and FR sisters. Since there was no effect of rearing conditions on the similarity between siblings, 500 bootstrap comparisons were made between males and females after NR and FR female offspring

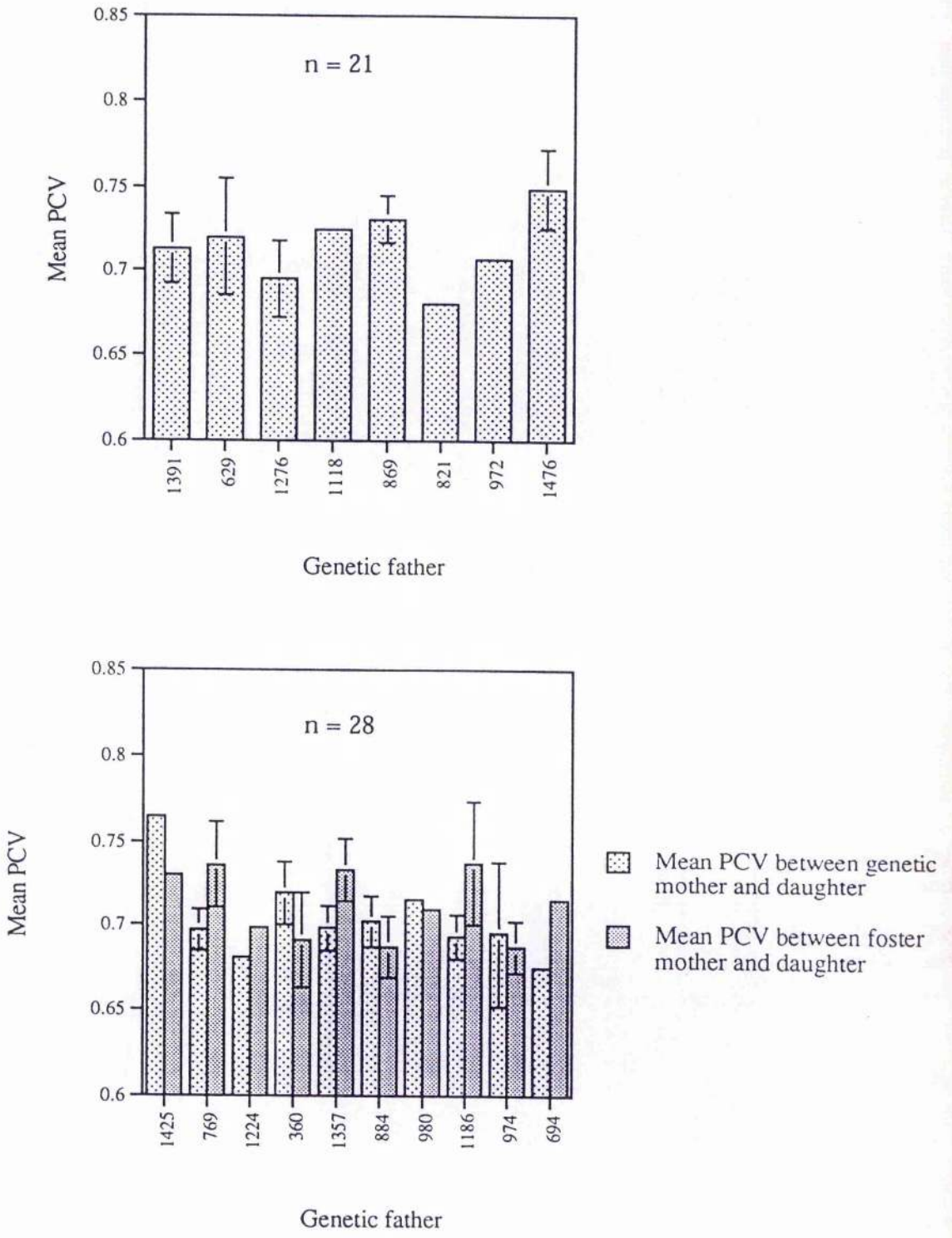


Fig. 2.7. & 2.8. Mean PCVs between mothers and daughters in normally reared (top) and foster reared (bottom) groups. The mean PCV is derived from the PCVs of mothers and each female offspring (standard deviation bars are shown).

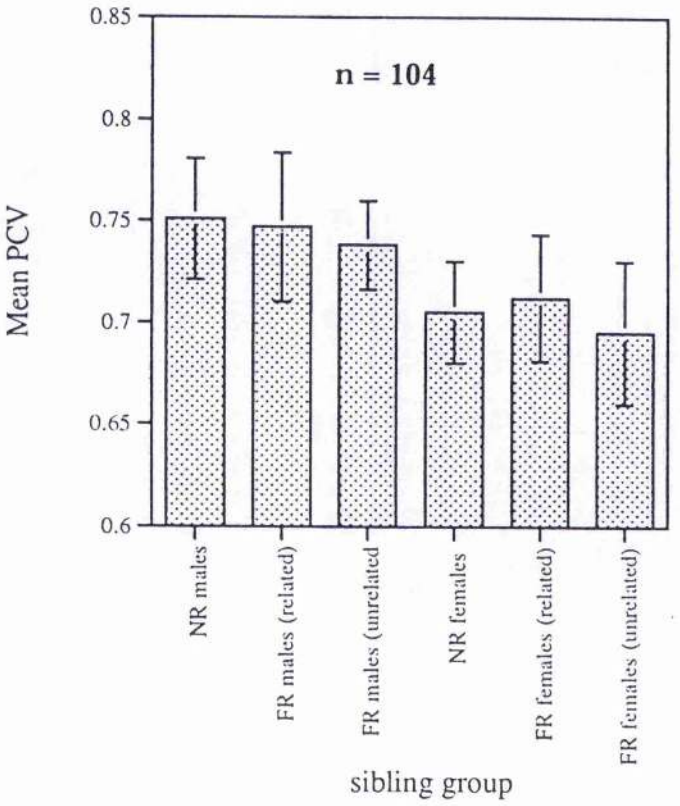


Fig. 2.9. Mean PCVs between male and female siblings from normally reared and foster reared groups. Groups labelled as related siblings refer to birds that were originally from the same clutch before fostering and were therefore genetically related, and those labelled unrelated were from different clutches before being being foster raised together and therefore not genetically related. The mean PCVs are derived from the average of each sibling group. Standard deviation bars are shown.

were grouped, and NR and FR males were grouped. Sisters were always significantly less similar in their calls than males ($z = 3.48$, $P<0.008$, 500 bootstraps).

The PCVs of same sex siblings were compared with the results of offspring and their same sex parents with which they were raised. In most cases, offspring were not significantly more similar to their siblings than to their same sex parents. The exception was for the foster-raised male offspring who were more similar to their brothers than to their foster fathers ($z = 2.10$, $P<0.05$, 500 bootstraps).

2.3.6. Order of similarity: who was most similar to whom?

Having compared each individual male and female offspring with its relatives (mother and father, both genetic and foster, and siblings), it was necessary to determine whether certain relationships would tend to exhibit a greater extent of call matching or inheritance.

Table 2.3. summarises each relationship in an order of similarity of the call, based on the mean PCV results of cross-correlations of the distance call. A rank has been assigned to each group comparison which indicates how closely the calls are matched. Several groups may share a rank because there was found to be no significant difference between them after conducting a bootstrap comparison.

The table shows that the greatest similarity in the distance call of related individuals, existed between male siblings (regardless of whether they were normally or foster-raised) and normally raised sons and their genetic fathers. Despite there being no significant difference in the PCVs of genetic fathers and their NR sons and foster fathers and their FR sons, NR male siblings were significantly more similar to each other than foster fathers and FR sons ($z = 2.88$, $P<0.008$, 500 bootstraps), and so they were assigned a rank of 2, together with mothers and the daughters they had raised, and

Group comparison	Mean PCV	Rank of similarity
NR male siblings	0.751	1
FR male siblings (related)	0.747	
NR genetic fathers & sons	0.741	
FR male siblings (unrelated)	0.738	
FR foster fathers & sons	0.724	2
NR genetic mothers & daughters	0.719	
FR foster mothers & daughters	0.714	
FR female siblings (related)	0.712	
NR female siblings	0.706	3
FR genetic fathers & sons	0.705	
FR female siblings (unrelated)	0.695	
FR genetic mothers & daughters	0.694	
NR genetic fathers & daughters	0.683	
NR genetic mothers & sons	0.677	4
FR genetic mothers & sons	0.674	
FR foster fathers & daughters	0.671	
FR foster mothers & sons	0.662	
FR genetic fathers and daughters	0.654	

Table 2.3. The rank of similarity between certain related individuals' distance calls. Mean PCV denotes the mean peak correlation value and is the result of cross-correlations between the calls of two individuals. These values were then averaged for each group to provide the mean PCV. PCVs between successive lines on the table have been compared by bootstrap analysis (500 bootstraps employed) to test whether there was any significant difference in the similarity of specific parent offspring or sibling relationships. All comparison groups within a rank had to be not significantly different in order to qualify in that rank, otherwise they were placed in the next rank down. A rank of 1 indicates the most similarity in the DCs, and 4 the least similarity between the individuals concerned.

foster-raised female siblings. The top two ranks of similarity of the DC therefore consist of siblings (excluding NR female siblings), and offspring with their same sex parents.

Thereafter, ranks 3 and 4 consist predominantly of comparisons between offspring and their opposite sex parents with no real tendency for mothers and sons to be more similar in their DCs than fathers and daughters or vice versa. Also included in rank 3 are NR female siblings, which are not significantly different from FR female siblings in rank 2, but are so with foster fathers and FR sons in this rank ($z = 2.32$, $P<0.05$, 500 bootstraps). Genetic mothers and their NR sons are top of the fourth rank because they differ from genetic fathers and FR sons ($z = 2.48$, $P<0.05$, 500 bootstraps).

Figures 2.10-2.12 show sonagrams of the DCs of examples of male and female offspring and their genetic and foster parents. Figure 2.10 illustrates clearly how normal raised offspring shared almost identical DCs with their genetic father. Similarly, females were very similar in the characteristics of their calls to their mothers, but as Figure 2.12 shows, foster mothers were as similar to their offspring as their genetic mothers that did not raise them. Figure 2.11 shows the DCs of male offspring and their foster and genetic fathers, and supports the findings of cross-correlation analysis in that males were more similar to the foster males that raised them than to their genetic fathers with whom they had had limited exposure.

2.4. Discussion

Despite earlier suggestions that the calls of estrildid finches were not prone to be affected by environmental influences during the development of the young (Güttinger & Nicolai, 1973; Price, 1979), more recent studies indicated that calls of male zebra finches were not predetermined, and were at least partially learned (Immelmann, 1969, 1972; ten Cate, 1982; Zann, 1984, 1985; Brindley, 1988; Jones, 1994).

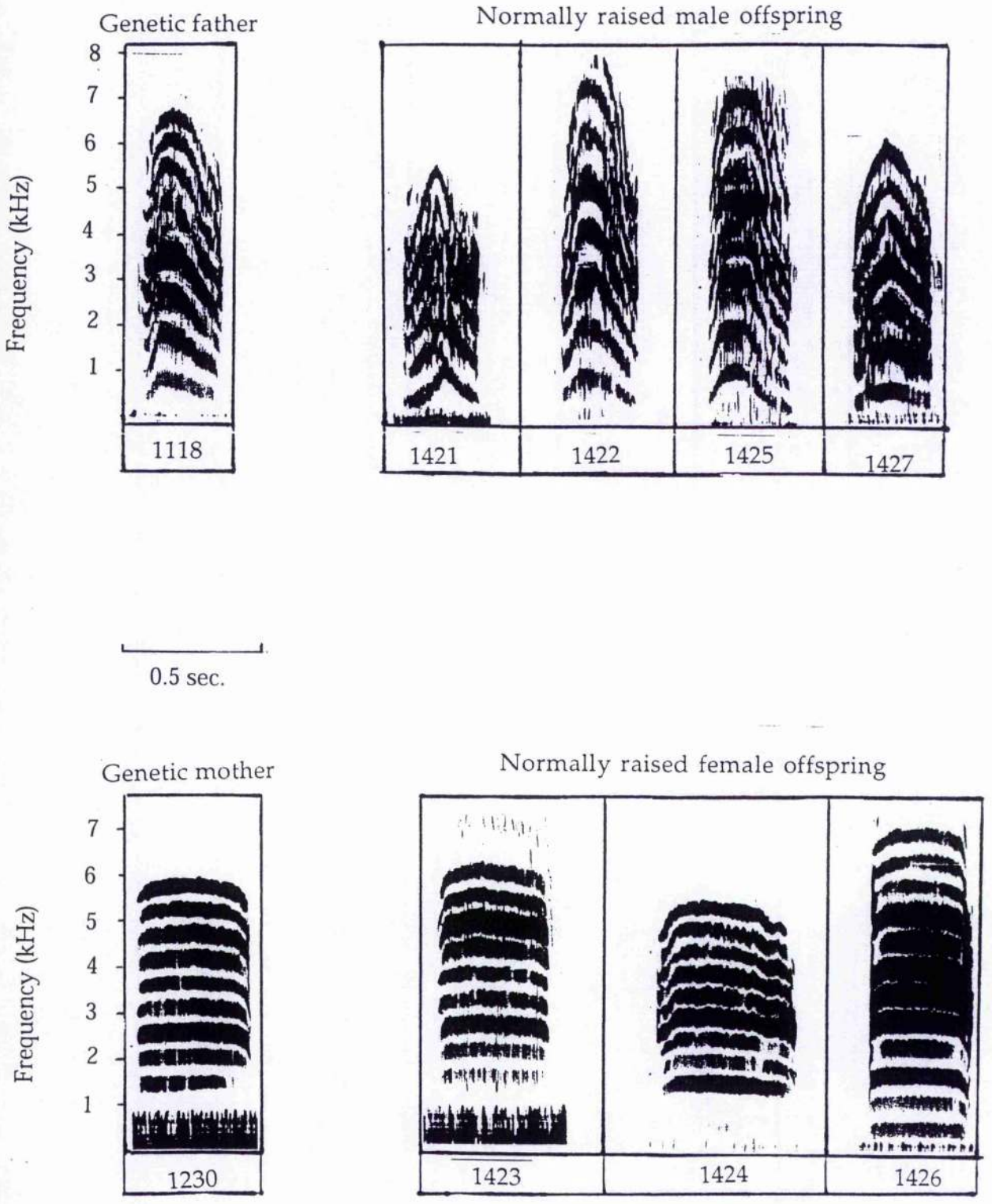


Figure 2.10 Sonagrams of the distance calls of normally raised male and female offspring and their genetic father and mother.

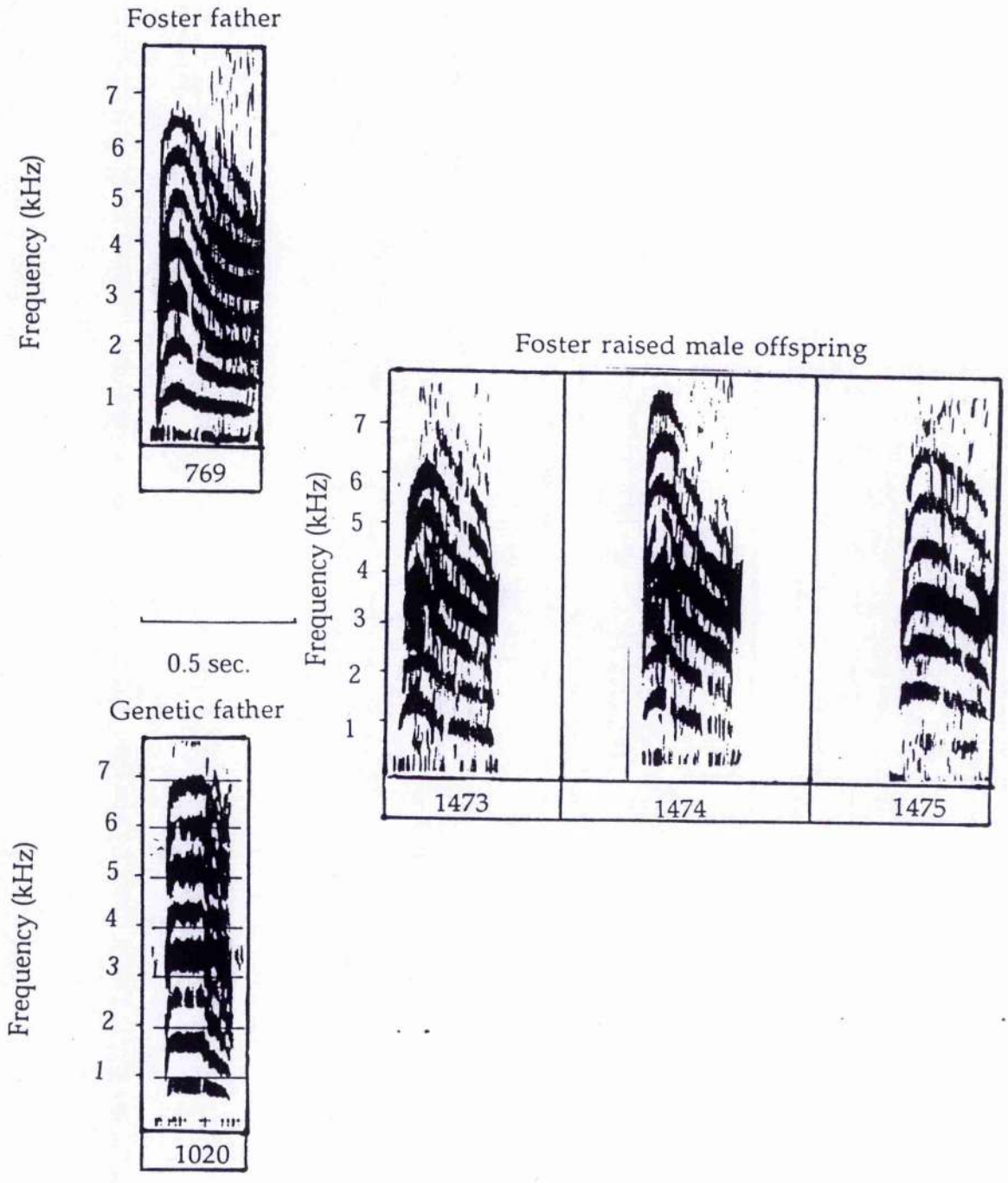


Figure 2.11 Sonagrams of the distance calls of fostered male offspring and their foster father (that raised them) and their genetic father.

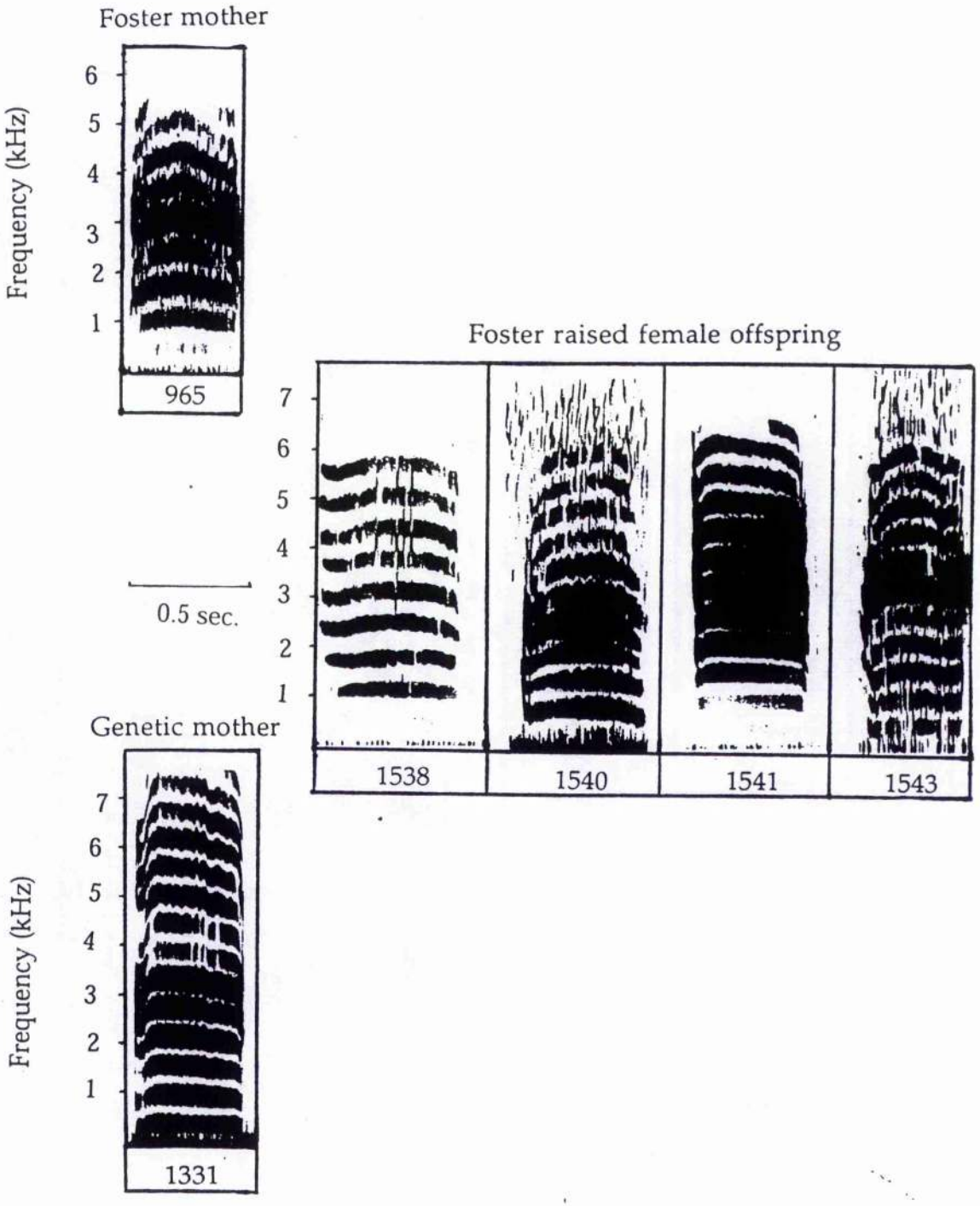


Figure 2.12 Sonagrams of the distance call of fostered female offspring and their foster mother (that raised them) and their genetic mother.

The precise genetic and environmental contribution on an individual's call phenotype is difficult to quantify, but fostering experiments may allow the experimenter to determine the extent to which learning can modify the calls characteristics of a young bird's vocalisations. By comparing the similarity of the calls of offspring to their genetic parents (which have passed on genetic material and thus will consequently share certain characteristics) and then to their foster parents (which can only affect call ontogeny by their own behaviour and vocal interactions with the offspring), it may be possible to assess which is the more salient factor in influencing the outcome of the call.

Zann's cross-fostering experiments with zebra and Bengalese finches (1985) were able to shed light on the learning tendencies of young birds with regard to the DC. The results of this study demonstrated that there are no clear rules determining who learns what from whom; some males learned the DC of a non-conspecific foster parent, whilst others acquired an abnormal conspecific DC even though they were not exposed to an adult zebra finch model.

Zann concluded that the template for the acquisition of the normal DC was open to certain environmental influences in zebra finch males but not females. He suggested that males may inherit fairly detailed species-specific specifications on certain parameters of the DC, but in some unusual circumstances (such as cross-fostering) these can be overridden by the specification "learn your father's DC", with the result that some FR males learnt the call of their Bengalese finch foster parents.

In the present experiment young zebra finches were not cross-fostered between two separate species, but were instead fostered to unrelated conspecific parents. Trends within and between normally reared and foster-reared families could be examined to detect whether DCs were more similar between related individuals in order to determine whether environmental or genetic influences were shaping the development of the call.

The fostering protocol was designed to control for the affects of multiple influences on the chicks development. An alternative procedure could have involved swapping half the clutch for a similar number in another pair's clutch, whilst retaining half with their genetic parents. This would have enabled a comparison between genetic and adopted offspring and their father. However, in doing so, experimental groups would have consisted of control (NR) chicks and fostered (FR) chicks, with a possible sibling influence on learning not being controlled for; any tendency for young birds to learn from one another could affect the DC in these birds in adulthood. Therefore we might find that DCs of FR males were more similar to the foster father than would be the case if all siblings were fostered, and consequently, NR males might be less similar to genetic fathers than would otherwise be so, simply because of the interaction with FR siblings, and the potential for sibling-sibling imitation. If this were true, the NR would not be the correct control for the FR chicks. The results of this experiment have shown that siblings (or rather nest-mates) share very similar DCs, suggesting that there may be some degree of imitation amongst young birds in a clutch, thereby justifying the protocol adopted.

Several clear trends were evident from the results. Offspring of both sexes were significantly more similar in the characteristics of their DCs to their same-sex parent; males' DCs matched their foster fathers more than their foster mothers, and matched their genetic fathers more closely than their genetic mothers. Similarly, females matched their foster mothers more than their foster fathers, and their DCs were more similar to their genetic mothers than their foster mothers. This is to be expected considering the DCs of either sex are sexually dimorphic and easy to distinguish apart from sonagrams.

The DCs of fostered offspring were more similar to the foster parents that had raised them than they were to their genetic parents. This already suggests that calls are learnt, and are, in any event, certainly prone to be under some environmental control.

Genetic fathers that had raised their own sons were comparatively more similar to them than foster fathers were to their unrelated male foster offspring. Since both these groups were raised under the same conditions and assuming that genetic fathers and foster fathers did not differ significantly in the type and amount of parental care offered, then this discrepancy in the PCVs of the two groups of fathers and sons is most likely to be due to a genetic influence.

As Zann explains, such a genetic influence need not necessarily predetermine that sons should produce calls like their genetic fathers, but would probably act more as a guide to what should be learnt. In the majority of FR males in Zann's experiment, the inherited specifications prevailed when the DCs of the foster parents failed to provide a noise element, and therefore did not conform to the 'template' of what should be learnt. Consequentially, in FR males it appeared that the DC changes continuously beyond the sensitive phase and maturation when the call should have stopped developing. The vocal output of FR males never satisfactorily matched the incomplete template.

Males that had been cross-fostered to non-conspecifics which subsequently lacked the appropriate vocalisations for normal development may indeed produce deficient DCs (Zann, 1985). However, this seems unlikely to account for the lower copying accuracy of birds that had been fostered to unrelated conspecific parents, as these did possess normal adult DCs, and would thus represent perfectly adequate models for copying.

In the present experiment, young birds were provided with adult zebra finch foster parents that possessed a normal DC. Therefore, to account for slightly higher copying accuracy of genetic fathers by their sons, by the action of inherited specifications of the

template, would be suggesting that young birds had a predisposition to learn characteristics of the call better from individuals that shared genes with them. So theoretically, if genes were influencing call learning, then either there is a genetic biased to the template that predisposes a bird to learn more from a related individual, or characteristics of the call are directly inherited.

It is unlikely that young birds inherit a specific template that they could match to the vocalisations of related individuals from day 1 post-hatching and without prior experience. A more likely mechanism would be that individuals use a simple rule, such as "treat anyone in the nest as kin", or to learn from those that a young bird grows up with (Krebs & Davies, 1981). Indeed, once an individual gains experience with particular conspecifics, it is able to learn and recognise vocalisations from even unrelated individuals: for example, the call matching of American goldfinches (Mundinger, 1970), and within pairs of crossbills (Groth, 1993). There are clearly several different interacting factors involved, but FR males would be expected to have copied the males that had reared them to the same degree as NR males.

Alternatively, considering the difference in the PCV of genetic fathers and sons, and that of foster fathers and sons is only just above the threshold at $P<0.05$, it is possible that young chicks were already learning their fathers vocalisations before they were fostered, or least, learning to recognise them. Parent-offspring recognition has been shown in several species and appears to occur at a very young age in order to facilitate recognition. By switching broods of nestling galahs of various ages between nests and observing their parents' behaviour, Rowley (1980) found that parent galahs (a species of cockatoo) could recognise their offspring but not until their last week in the nest. The likelihood of post hatching zebra finch chicks acquiring information on their parents vocalisations probably increases with every day in the nest, so that chicks that were swapped with other clutches at day 13, may already be forming the first rudimentary memorisation of their fathers distance call. If learning had begun before the chicks were

removed from their genetic parents, then fostering a young bird to another conspecific adult model with a distinctively different call may have retarded the learning of the new male's call enough to result in a lower matching accuracy and therefore a less similar call to the foster father.

The precise delineation of the sensitive phase of call learning has been studied in several experiments. In Zann's cross-fostering experiments, the duration of parental contact for 40 or 60 days appeared to have no effect on the outcome of how much was learnt, leading Zann to conclude that the sensitive phase must terminate prior to 40 days of age.

Slater and Jones (1995) did not, however, find any evidence that the DC was learned earlier and the song later. They found that young males that had been reared with their fathers until day 35 and then caged with a different male, did not tend to learn the DC of their father and the song of their tutor, but preferred to copy both song and the call from the same model, whether that model was a bird encountered before or after 35 days. This appears to contradict the findings of Zann (1990) that within a family, DCs were conserved more strongly than song down the generations, but Slater and Jones (1995) suggest that this could simply be due to the fact that DCs are less variable and therefore it would be easier to find a matching tutor than for song, rather than because of any transmission through kin.

Brindley (1988) removed fathers from their clutches at various ages and found that males who experienced an adult male after 25 days produced a more characteristically male call than those that had been separated at 25 days or earlier. In a further experiment Brindley raised young males with their father until 35 days, then presented the young with both the father and a second adult male tutor behind a mesh screen and found that there was a preference for learning the calls of the father. At 70 days, the

father and another tutor were added to birds whose father had been removed at 6 days, and their calls re-recorded at 105 days. No change was found in the structure of the call.

Brindley's results suggest that zebra finches have a sensitive phase for call learning, rather like that for song learning, and that the father, heard prior to this period, is the preferred tutor when a choice of adult males are presented during sensitivity. In these experiments, it was suggested that the sensitive phase was after day 25. However, if zebra finches are able to distinguish calls heard prior to 6 days from those of novel ones heard later in their development, and then exhibit a preference for the tutor which gave these calls, then this could account for the higher PCVs of genetic fathers and sons compared to foster fathers and sons.

It is, however, possible that the lower PCVs observed between foster fathers and sons compared to genetic fathers and sons were merely the consequence of the level of disruption that the two groups experienced. Despite all the birds being successfully fostered, there would nevertheless have been slight changes, at least temporarily, in the behaviour of parents and offspring following the swap. This may have resulted in the parents not spending as much time at the nest as the genetic parent counterparts, perhaps not feeding the chicks as much, and maybe not vocalising to the same extent, which might well have been enough to affect call learning in the chicks.

There was not such a difference between genetic mothers and their daughters, and foster mothers and the female offspring they raised. Indeed there was no significant difference in the PCVs of genetic mothers and daughters and foster mothers and daughters. This could be because, as suggested by Zann (1985), the template for the acquisition of DCs is not open to certain environmental influences in females as it is in males.

Unfortunately, most studies of sensitive phases of the calls in zebra finches have concentrated on delineating the timing of young males' learning, without consideration

of when and to what extent females learn calls. Zann (1985) has studied the ontogeny of calls in both sexes in some detail and observed that by day 35-40, the adult version of the DC in females is complete. In contrast, the male's DC undergoes further changes, most notably in frequency modulations, so that it does not become fully developed until 60-80 days after hatching. Females lack the noise element of the adult male DC, which is gained at around 60 days or so. It seems probable that any inaccuracies in copying that have arisen by, for instance, the disruption caused by fostering, will manifest themselves more in males whose vocal development extends for some 40 days past that of females, and which need to undergo more complex frequency changes to the basic tonal call of young fledglings.

In the present experiment, male siblings were found to be the most similar in their DCs, regardless of whether they were normally or foster-reared. For NR males, it is perhaps not at all surprising, since these birds would have been exposed to the same degree of environmental and genetic influence, and the outcome of their calls would therefore be expected to be most similar. FR siblings however, included non-related nest mates which had been fostered from another clutch, as well as genetic siblings, yet these birds do not show a significantly lower degree of call matching than related sibs. This may be an indication that the call is not predominantly affected by a genetic influence.

In Zann's study, some 30% of NR sons gave DCs that were identical to those of their fathers. This conclusion was based on the measurement of four parameters of the DC and comparing these with conventional statistical tests. In this study the DCs of individuals were compared using a cross-correlation technique which considers the shape of the call as a whole, and compares this in a time domain with another call. The degree of overlap is measured as a peak correlation value (PCV) which relates directly to the degree of similarity between the two calls.

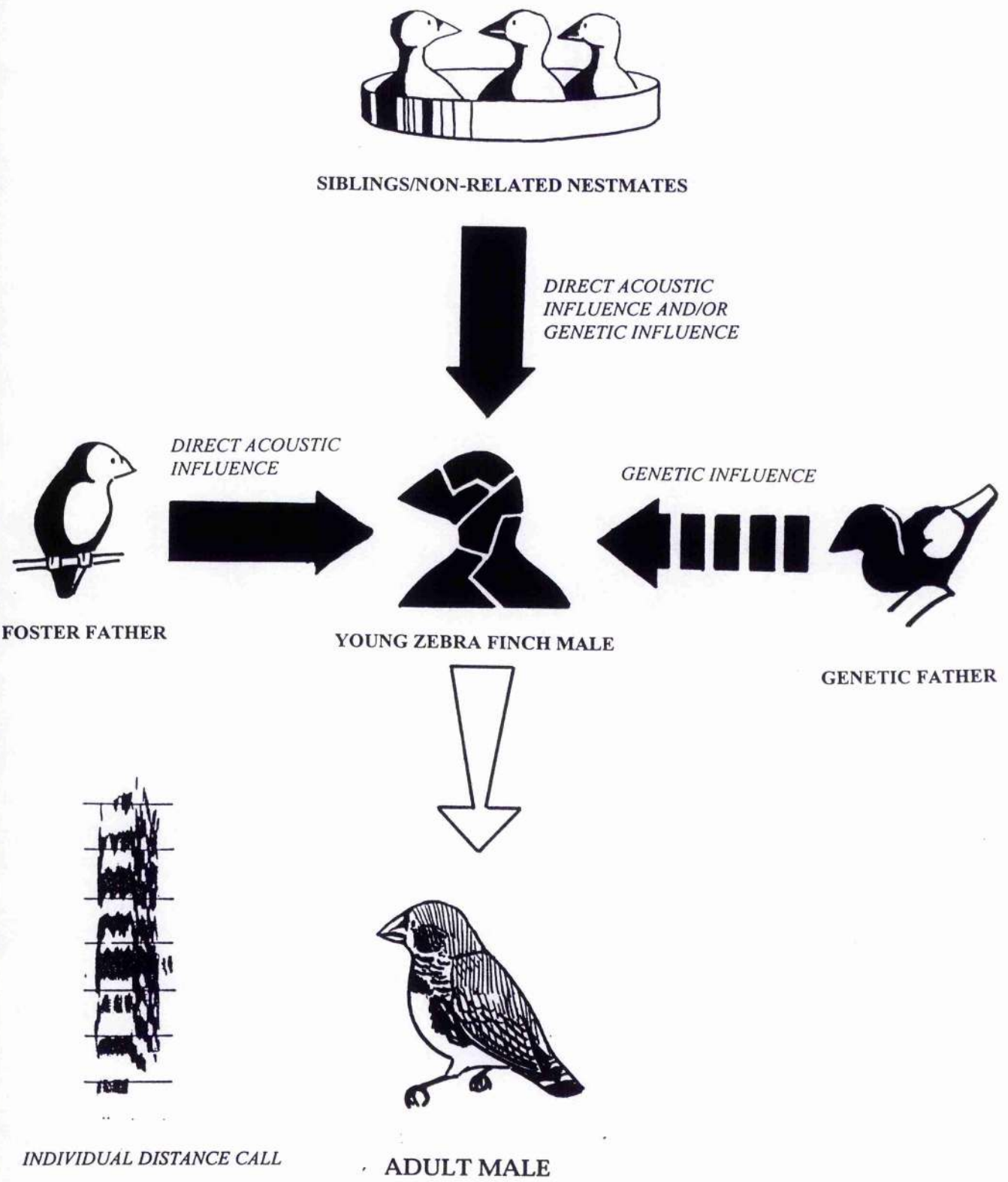
It is perhaps a justification for using this method that the PCVs observed did not show any calls to be identical because of the accuracy in assessing the overall characteristics of the call and not merely a few select parameters. In considering the overall shape of a call, cross-correlations are, in theory, more akin to analysing calls by eye, though in a less subjective way, and allows similarity to be compared between pairs of individuals in a quantifiable manner. Zann's choice of parameters of the DC to measure may be justifiable in that they were the characteristics which appeared to be most variable in individuals and more likely to reflect the extent of learning, but to claim that the DCs of fathers and sons were identical without accounting for all parameters of the call may be regarded as optimistic.

Zann's findings from his cross-fostering experiments have shown that young zebra finches are prone to be affected by environmental influences during their development, most notably their parents' vocal behaviour, but that these birds are also guided to a certain extent, by a genetic predisposition to learn specific vocalisations that are more appropriate than others (i.e. to recognise the correct species, sex and, perhaps less likely, even the individual to learn from).

The results of this experiment reflect those of Zann in that young zebra finches appear to learn more from certain tutors, based on sex, and relatedness, and that there is a difference between the sexes in the extent to which learning is apparently affected by environmental and genetic factors (see Fig. 2.13 for a summary of possible factors affecting a young birds call).

The biological significance of this developmental scheme is open to speculation, but there is evidence to suggest that calls may be used by conspecifics to impart information of individual identity. Miller (1979) showed that females can discriminate the song of their fathers from others, and Zann (1985) reports evidence that the DC is recognised by the sexual partner. If the capacity for individual recognition is available, and as this

Fig. 2.13 Diagram summarising probable influences on the development of a young zebra finches adult distance call



study has confirmed, related individuals tend to have similar calls, then there is good potential in zebra finch calls for kin recognition to occur.

CHAPTER 3

INVESTIGATING EVIDENCE FOR VOCAL PLASTICITY IN THE DISTANCE CALL OF ADULT ZEBRA FINCHES RAISED UNDER VARYING SOCIAL CONDITIONS

3.1 Introduction

Until recent studies have shown otherwise, species of birds that learn their vocalisations have tended to be categorised as either age-dependent learners or age-independent learners. Age-dependent learners, also known as age-limited learners, are defined as those species that learn their songs during a particular period in their development which is termed the sensitive phase. After this sensitive phase, which occurs prior to reaching maturity, the song remains relatively fixed in adulthood and the ability to learn new vocalisations is absent. In age-independent learners there is no constraint in when the song has to be learnt and their potential for the acquisition of new elements or songs remains throughout their adult lives.

The distinction between these two systems may not be as clear as was previously assumed, since some studies on age-limited passerine species have shown that under certain circumstances, new songs can be learnt after the sensitive phase (Eales, 1985; Baptista & Petrinovich, 1986). Slater *et al.*, (1993) question whether there are such species as age-limited learners, and suggest that, in those studies that showed a failure to learn later, the reason may have been a lack of a sufficient stimulus. For instance, young white-crowned sparrows (*Zonotrichia leucophrys*) only learn from taped conspecific playbacks if they are presented between the sensitive phase of 10 to 50 days (Marler, 1970). Baptista & Petrinovich (1986) were able to extend the sensitive phase of learning in the same species by using the more salient stimuli of live tutors.

In their paper, Slater *et al.,* (1993) discuss the results of a study they carried out which examined more closely the interaction between early experience and later learning (Slater *et al.,* in press). Although young male zebra finches would preferentially learn from tutors they were exposed to during the sensitive phase of 35 to 65 days, those individuals deprived of a tutor at this time would recall elements from their father's song when they were fledglings. They also showed evidence that males without adult tutors to partially modify their songs in accordance with the other young males in their group. In addition, birds that had been female-raised only and had experienced extreme social deprivation by isolation from 35 days to 120 days, demonstrated some degree of vocal plasticity by dropping or gaining elements in their songs when later presented with tutors. From these more recent studies there is no doubt that age-dependent learners, such as the zebra finch (*Taeniopygia guttata*), have a greater degree of plasticity than earlier studies (e.g. Immelman, 1969) suggested.

The number of relevant studies on the plasticity of call note learning is comparatively small, but it is possible to form hypotheses from the theories and results of song learning literature. Call imitation is well documented in Psittaciformes and is an integral part of song learning in many passerines (Marler and Mundinger, 1971), vocal imitation is also responsible for the closely matched flight calls in mated pairs of several cardueline finches (Mundinger, 1970; Marler & Mundinger, 1975; Mundinger, 1979). In duetting species, mated pairs may share common calls through mutual imitation (Grimes, 1966; Wickler & Seibt, 1980) or be capable of reproducing the full duet in the absence of their partner (Thorpe & North, 1965, 1966).

Nowicki has shed much light on the subject of vocal plasticity in calls by his captive studies and field observations on black-capped chickadees (*Parus atricapillus*). By recording the calls of several wild flocks which were geographically separated, and then rearranging the flock membership into captive flocks of strangers, he was able to observe convergence between individuals as indicated by a decrease in the variance of

the temporal and spectral parameters that were measured (Mammen & Nowicki, 1981). In a later study (Nowicki, 1983) he found that convergence occurred through mutual imitation and that the rate of acquisition of the new group specific call was less than one week. These studies have, however, merely demonstrated that some species of passerines are not age-limited in the learning of their calls, just as there are age-independent song learners. As such they do not show evidence for prolonged vocal plasticity in an age-limited learner.

Zebra finches are ideal subjects in which to investigate the possible existence of vocal plasticity and call convergence for several reasons; they were previously classed as age-independent song learners (though the distinction appears to break down with this species), their distance calls are thought to be at least in part learnt from the father in a sensitive phase before day 40 (Zann, 1985), and these distance calls remain relatively stable thereafter in adulthood. The studies of Eales (1985, 1987) and Slater *et al.* (1993) have shown that the stability of vocalisations learnt during the sensitive phase is not by any means robust, especially when young birds are not exposed to the appropriate adult male tutors during their early development.

In chapter 2, there was an indication that certain young zebra finches could match their DC more closely to male models that they were related to. The environmental conditions that a young bird experienced are also likely to be influential on the crystallised call that it produces in adult life.

The first experiment will examine whether DC convergence can occur in normally-raised adult male zebra finches if they are confined to a close social group. The second experiment will examine if call convergence occurs to a greater extent in adult males that have not experienced an appropriate male conspecific model during their development. The third experiment will investigate whether similarly deprived males

with abnormal vocalisations will undergo a change in their distance calls if provided with a suitable tutor as adults.

3.2 Methods

3.2.1 Experiment 1: Investigating evidence for call convergence in normally raised adult male zebra finches

3.2.1.1 Subjects

A total of 12 adult male grey morph zebra finches (*Taeniopygia guttata*) were selected from a captive laboratory population. All birds had been normally raised by their parents in an animal house until independence at 35 days, when they were placed into separate cages with other males of a similar age. A sample of at least 20 calls were recorded in a sound attenuation chamber when the birds were 120 days of age. The Kay DSP Digital Sonagraph 5500 was used to analyse the sonagrams of the distance calls (the loudest, longest type of call emitted by a zebra finch when visually isolated from conspecifics). All birds recorded were judged by eye from sonagrams to possess individually distinct distance calls (DCs) that were characteristic of a normally raised captive male of the species.

3.2.1.2 Procedures

The 12 zebra finches were separated into three experimental groups, consisting of four males in each, as near to 120 days as possible. It was ensured that none of the four birds in each group had had previous experience of one another to control for any effect of

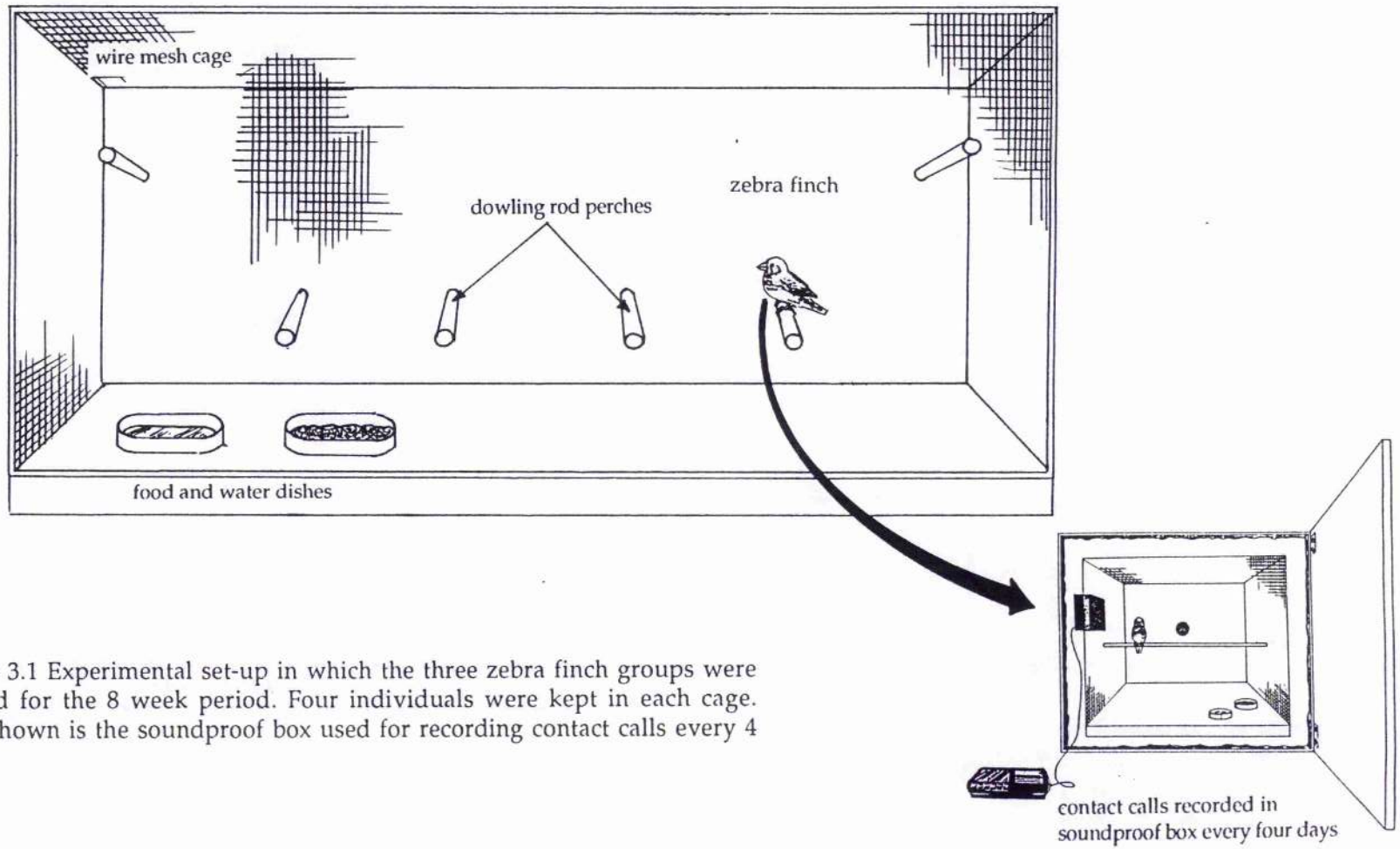


Figure 3.1 Experimental set-up in which the three zebra finch groups were housed for the 8 week period. Four individuals were kept in each cage. Also shown is the soundproof box used for recording contact calls every 4 days.

familiarity on an individual's call development or any influence it may have had on predisposing the process of call convergence.

Each group was housed in a cage 50 x 150 x 50 cm fitted with four horizontal dowling rod perches (see Fig. 3.1), and the cages were kept in separate rooms to visually and acoustically isolate them from other conspecifics. None of the birds therefore had any contact with any conspecifics other than its three cagemates for the eight weeks of the study. Birds were fed and watered daily and received a 14/10 light/dark cycle.

3.2.1.3 Recording and analysis of distance calls

The three experimental groups were kept in isolation for 8 weeks, during which time each individual was recorded at 4 day intervals in a sound attenuation chamber fitted with a Sennheiser MD 400 microphone (frequency response of microphone 1000 - 10 000 $\pm$ 6dB) and speaker for conspecific playbacks (see Fig 3.1). The speaker was used for playing the calls of other zebra finches that had been recorded in an animal house, in order to stimulate the subject into a calling response. Conspecific playbacks were only played for a maximum of five seconds once or twice. This procedure was followed as a last resort to obtain a sample of distance calls from birds that remained silent and the exposure to the conspecific playback was not considered lengthy enough to have any confounding affect on the strictly controlled isolation of each group.

Each recording session lasted approximately 10-15 minutes, during which a sample of approximately 20 DCs were collected. Calls were recorded using a Marantz CP 430 recorder and were analysed initially by eye on a Kay DSP Digital Sonagraph (sampling rate of 20kHz; upper frequency limit of 8kHz) to separate the DCs from all other vocalisations and make a subjective assessment of whether call convergence had occurred. Objective analysis was carried out by cross-correlation of the digitised

sonagrams of the calls using Engineering Design's SIGNAL (version 3.0) software (see Appendix A.2.1 for description of the method of analysis). Of the sample of 20 DCs collected at each recording session per bird, the five clearest recordings were selected to be used in the cross-correlation analysis.

3.2.2 Experiment 2: Investigating evidence for call convergence in female-raised adult male zebra finches

3.2.2.1. Subjects

A second experiment was carried out with 12 adult male zebra finches that had been socially deprived during their early development. A total of 15 adult pairs of normal grey zebra finches were allowed to breed in cages, lay and incubate a clutch. The same conditions of rearing applied as in experiment 1, except the father was removed on the day that the first chick was hatched. On the same day the whole cage was moved from the breeding room to another isolated room so that the chicks would not hear the sound of an adult male zebra finch at any point. This procedure was repeated with each pair on the hatching of the first chick in the clutch. The females were then allowed to raise the brood through fledging to independence at about day 50, when all young males were moved to another room and housed with their siblings in cages.

3.2.2.2. Procedures

Twelve of the male offspring of 120 days of age were selected and separated into three groups of four individuals. The same procedure as in experiment 1 was followed, ensuring that cagemates were neither related, nor had any previous experience of the other young males prior to the experiment. The choice of cagemates also involve

housing birds together that had clearly distinct DCs from each other to assist in the detection of any call convergence amongst them.

The birds' DCs were recorded before the experiment in a sound attenuation chamber and thereafter every four days for a period of eight weeks. Comparisons were made between normally raised zebra finches and those raised under conditions of social deprivation without appropriate male tutors, to investigate whether a bird's developmental experiences would determine the level of vocal plasticity in adulthood.

3.2.3 Experiment 3: Investigating evidence for vocal plasticity in female-raised male zebra finches exposed to appropriate tutors in adulthood

Following experiments 1 and 2, where zebra finches that had been raised in either a normal laboratory or a socially deprived environment, were housed with similarly experienced conspecifics to test if call convergence would occur, a third experiment was conducted to test whether female-raised birds that had lacked salient adult male stimuli as young would be capable of changing their abnormal calls in adulthood if provided with a suitable model.

A further 12 male zebra finches were raised under similar socially restricted conditions to those in experiment 2. Of a total of 23 young birds available (approximately 120 days old), 12 were selected and housed in three groups of four as in the experimental protocol of experiment 2, except that in addition, a mature adult male was provided as a potential tutor. The tutor had a normal male distance call and was not related to or experienced with its tutees prior to the study. The experiment was run for 8 weeks and the DCs of all individuals were recorded every 4 days. Cross-correlations between the subjects and tutors were carried out on the SIGNAL (version 3.0) software to detect any changes in the DCs over time.

In order to ascertain if the zebra finches from both normally raised and female-raised groups had changed their calls over the 8 weeks of the experiment, it was necessary to examine whether there were any differences in the structure of the distance call at every four day interval when compared to the initial recording made from each bird prior to the commencement of the study. A sample of five examples of the DC were recorded from each individual and each in turn was compared by cross-correlating to five examples from the initial recordings; resulting in a total of some 25 cross-correlation comparisons. A mean peak correlation value (PCV) was obtained from the results of the 25 comparisons for every 4 day interval. These values represent how similar the DC is at each 4 day interval to the DC before the birds were placed together; a maintained decrease in the PCV over time would indicate that the call was becoming more dissimilar and may suggest that convergence was occurring.

3.3. Results

Figures 3.2.1-3.4.4 and figure 3.5.1-3.7.4 show the mean PCVs for each of 12 zebra finches over the 8 week period in the normally-raised and female-raised groups respectively. From these graphs there is no tendency for the PCV of any normally-raised males to increase or decrease significantly, indicating that the DCs recorded at each 4 day interval had not changed significantly from the initial recording before the experiment was commenced. Similarly there was no deviation in the structure of the DC in female-raised birds over the duration of the study, suggesting that cagemates had not altered their calls and not converged with each other.

Statistical comparisons were made between consecutive 4 day intervals using the samples of 25 PCVs for each individual at each session. A bootstrapping comparison (see previous chapter for description of bootstrapping technique) was carried out for

Fig. 3.2.1 - 1436

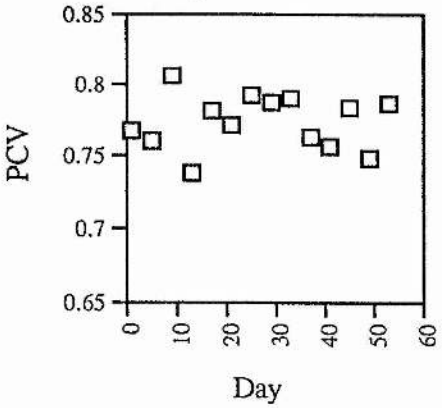


Fig. 3.2.2 - 1428

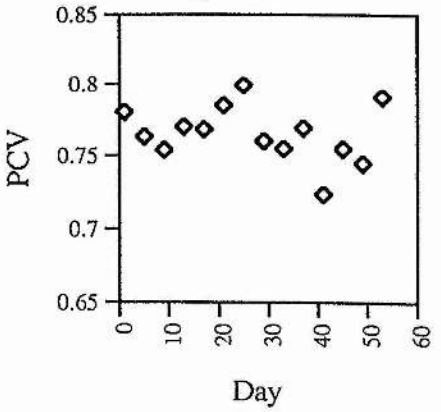


Fig. 3.2.3 - 1449

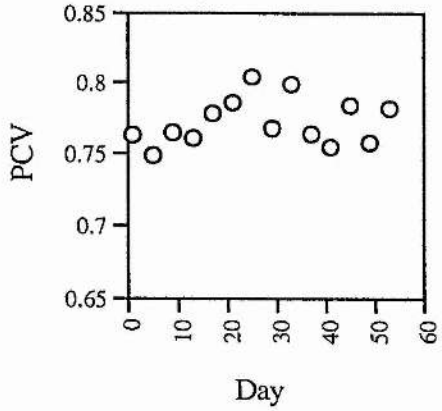


Fig. 3.2.4 - 1385

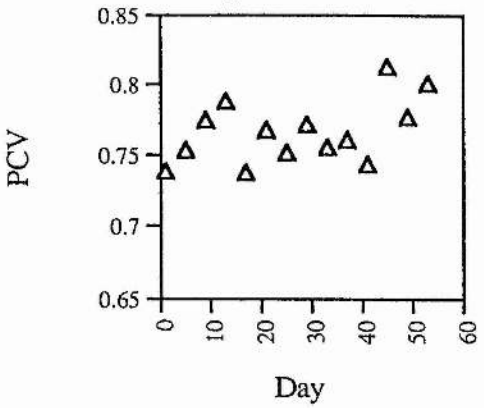


Fig. 3.2.1 - 3.2.4 Individual changes in distance call over time for normal-raised male zebra finches in Group 1. Each graph traces the change in the distance call for each individual. PCV represents the mean peak correlation value derived from 25 cross correlation comparisons between a sample of distance calls recorded every 4 days and a sample of initial recordings of the DC before commencement of the experiment.

Fig. 3.3.1 - 1415

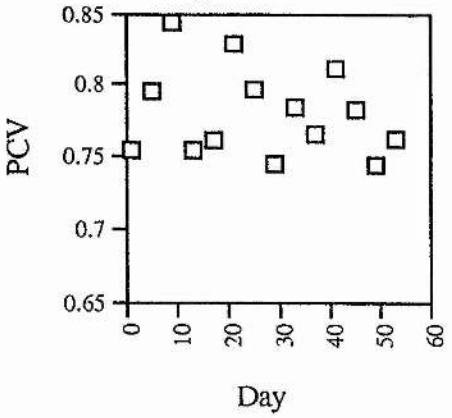


Fig. 3.3.2 - 1392

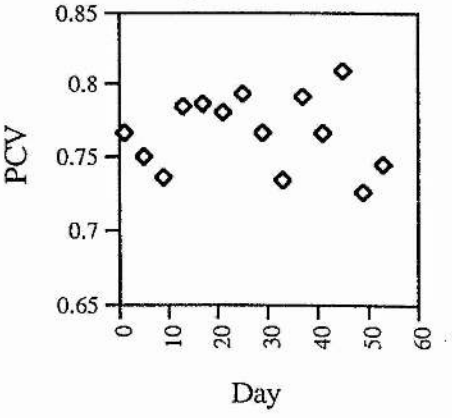


Fig. 3.3.3 - 1408

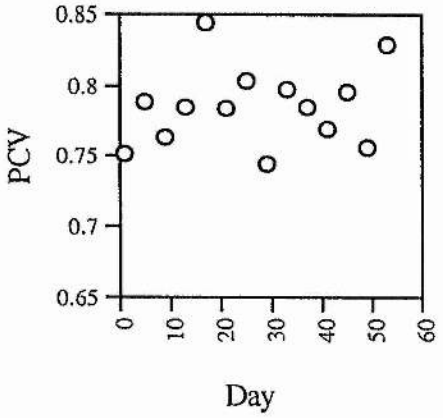


Fig. 3.3.4 - 1389

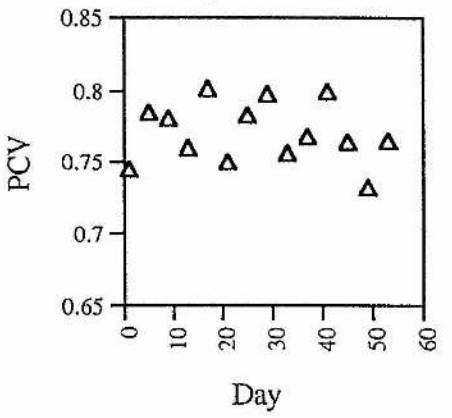


Fig. 3.3.1 - 3.3.4 Individual changes in distance call over time for normal-raised male zebra finches in Group 2. Each graph traces the change in the distance call for each individual. PCV represents the mean peak correlation value derived from 25 cross correlation comparisons between a sample of distance calls recorded every 4 days and a sample of initial recordings of the DC before commencement of the experiment.

Fig. 3.4.1 - 1440

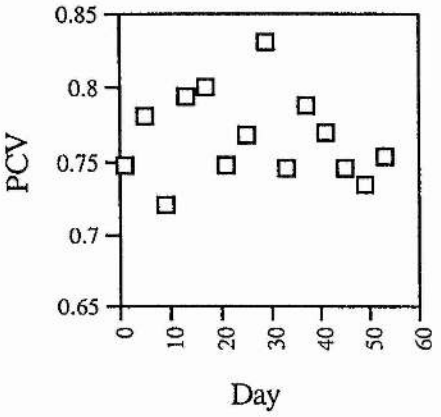


Fig. 3.4.2 - 1491

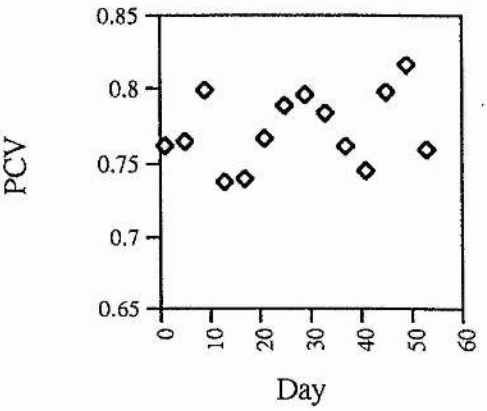


Fig. 3.4.3 - 1388

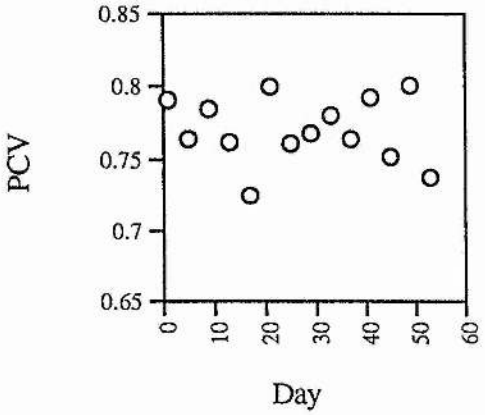


Fig.3.4.4 - 1394

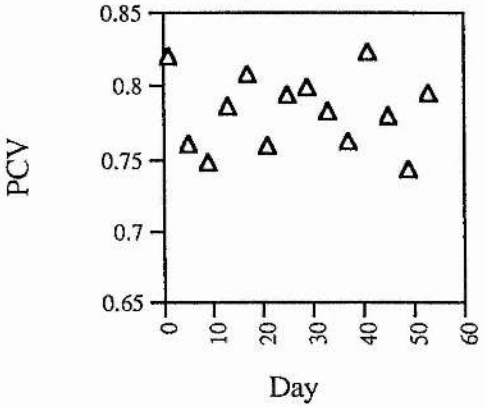


Fig. 3.4.1 - 3.4.4 Individual changes in distance call over time for normal -raised male zebra finches in Group 3. Each graph traces the change in the distance call for each individual. PCV represents the mean peak correlation value derived from 25 cross correlation comparisons between asample of distance calls recorded every 4 days and a sample of initial recordings of the DC before commencement of the experiment.

Fig.3.5.1 - 1490

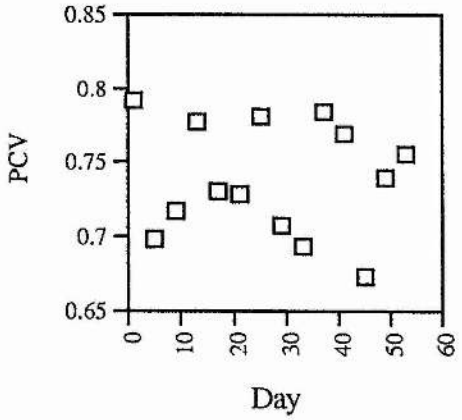


Fig.3.5.2 - 1455

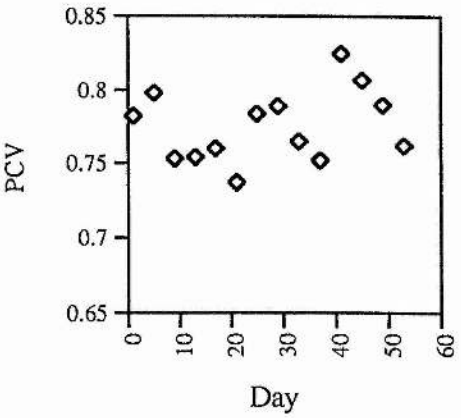


Fig.3.5.3 - 1450

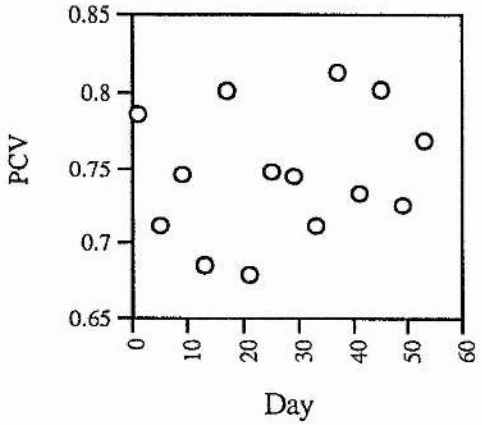


Fig. 3.5.4 - 1465

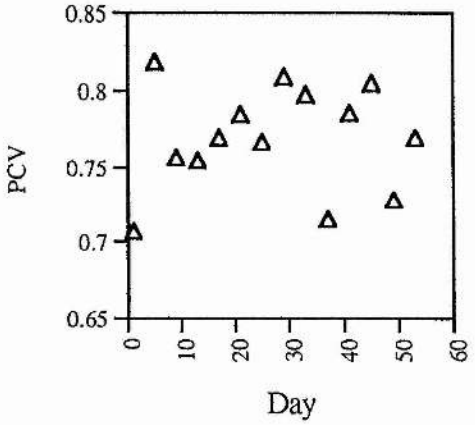


Fig.3.5.1 - 3.5.4 Individual changes in distance call over time for female-raised male zebra finches in Group 1. Each graph traces the change in the distance call for each individual. PCV represents the mean peak correlation value derived from 25 cross correlation comparisons between a sample of distance calls recorded every 4 days and a sample of initial recordings of the DC before commencement of the experiment.

Fig. 3.6.1 - 1386

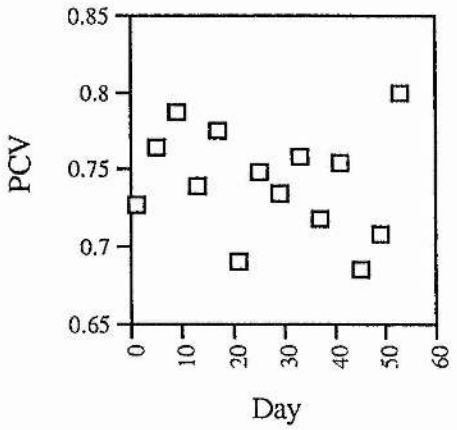


Fig. 3.6.2 - 1433

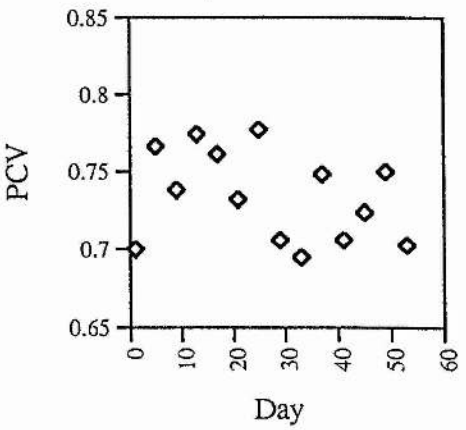


Fig. 3.6.3 - 1410

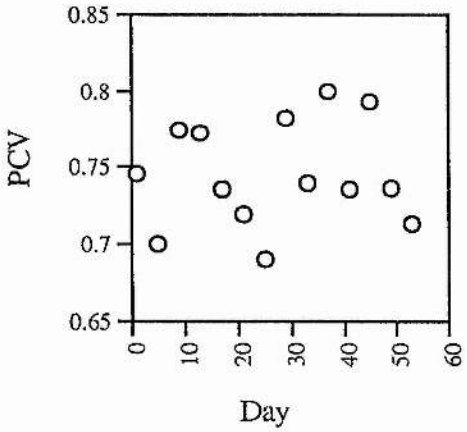


Fig. 3.6.4 - 1367

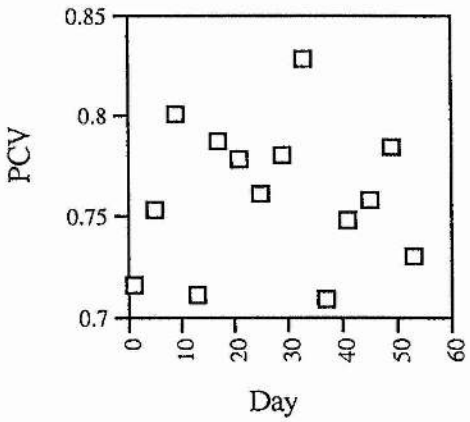


Fig. 3.6.1 - 3.6.4 Individual changes in distance call over time for female-raised male zebra finches in Group 2. Each graph traces the change in the distance call for each individual. PCV represents the mean peak correlation value derived from 25 cross correlation comparisons between a sample of distance calls recorded every 4 days and a sample of initial recordings of the DC before commencement of the experiment.

Fig. 3.7.1 - 1387

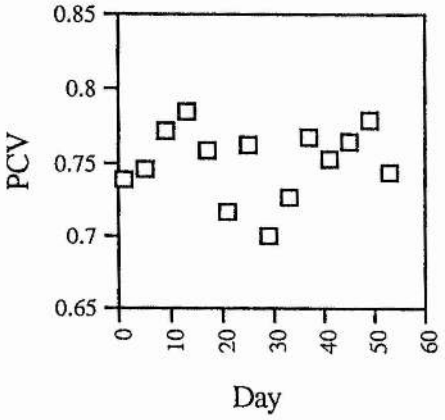


Fig. 3.7.2 - 1370

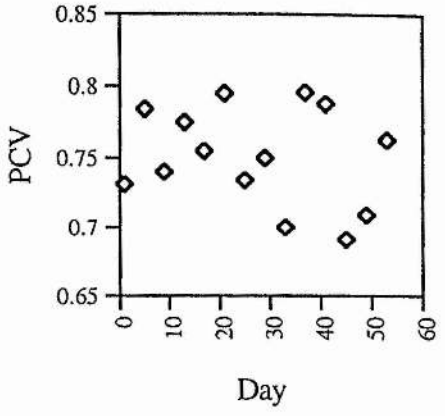


Fig. 3.7.3 - 1512

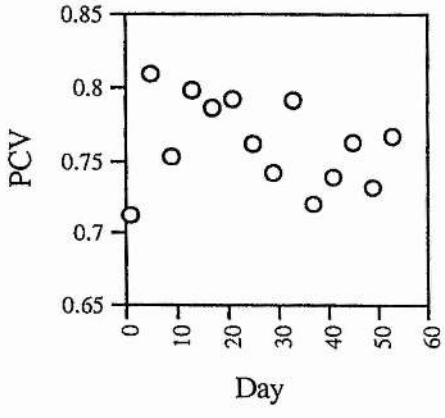


Fig. 3.7.4 - 1473

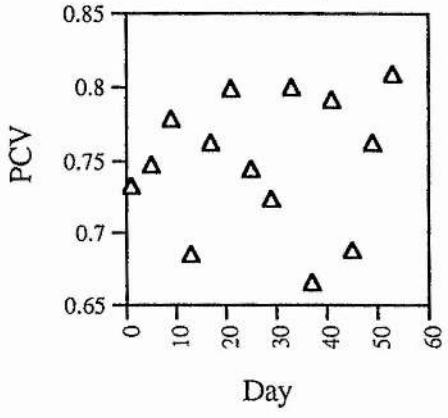


Fig. 3.7.1 - 3.7.4 Individual changes in distance call over time for female-raised male zebra finches in Group 3. Each graph traces the change in the distance call for each individual. PCV represents the mean peak correlation value derived from 25 cross correlation comparisons between a sample of distance calls recorded every 4 days and a sample of initial recordings of the DC before commencement of the experiment.

each bird between peak correlations for day 1 and day 5. The computer was instructed to repeat the bootstrapping 500 times, after which a z-score was calculated for each pairwise comparison. This procedure was then repeated between days 9 and 13, days 17 and 21, days 25 and 29 and so on, so that a total of seven timewise comparisons were made for each individual covering the 8 weeks of study. A comparison between day 1 and day 53 was also conducted to ensure that there was no discreet change in PCVs that may have been too subtle to be apparent within the span of a 4 day period comparison. Since all z-scores, encompassing both normally-raised groups and female-raised groups, were below the value 2.58 at $P = 0.01$, there was no need to reduce the alpha level to reduce the chances of a Type I error occurring. Therefore there was no statistical significance between the PCVs at each recording session (i.e. there was no significant change in the DC which might suggest that convergence had occurred).

The PCVs presented in figures 3.2.1-3.4.4 and figures 3.5.1-3.7.4 have been pooled for all 12 individuals in each group and the mean values for each 4 day interval represented in fig 3.8.1 for normally-raised and fig 3.8.2 for female-raised birds. These graphs show more clearly how the DCs of all individuals in both treatment groups were not affected over the 8 weeks. Indeed, the PCVs for normally-raised birds which possessed what might be referred to as a 'characteristic' DC for a laboratory bred male zebra finch, fell within the range of approximately 0.81 and 0.73. The mean PCVs of female-raised males, which possessed an abnormal and in some cases a female type DC, were slightly lower overall than their normally-raised counterparts within a range of 0.79 and 0.69. A bootstrapping analysis between the two groups revealed that this difference is significant ($z = 3.83$, $P < 0.01$). Therefore, although no individuals showed any overall tendency to significantly change their calls, there were notable variations in the structure of the recorded calls with a greater tendency for dissimilarity in individual DC samples in the female-raised group. The stereotypy of DCs in female-raised birds can therefore said to be less persistent than 'normal' males whose DC tend to be more stable between recording sessions as suggested by the higher PCVs.

Fig. 3.8.1 - normally-raised

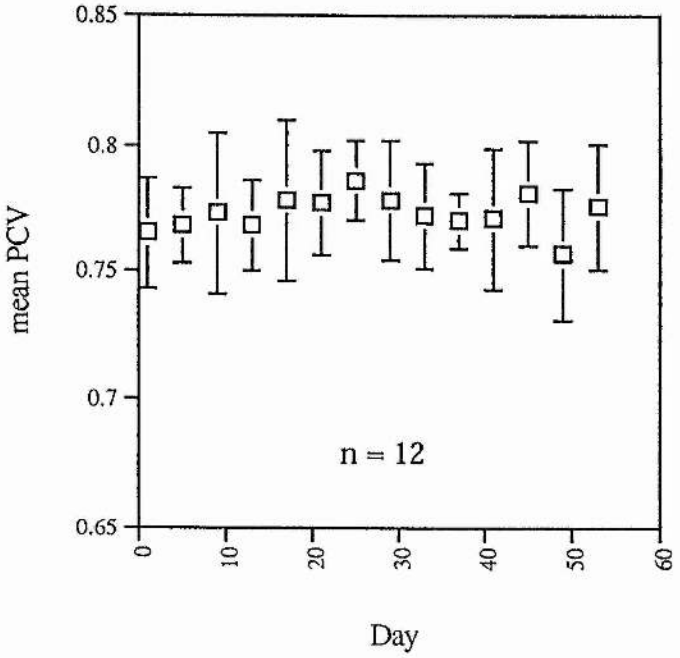


Fig. 3.8.2 - female-raised

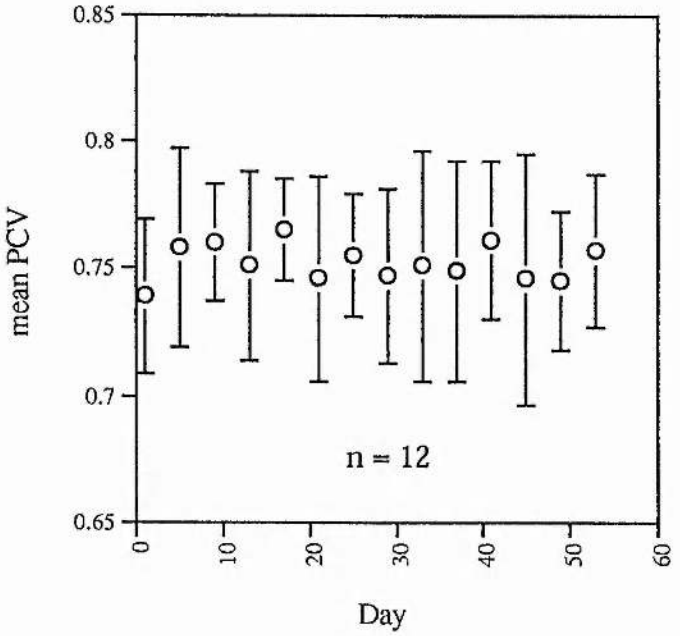


Fig.3.8.1 - 3.8.2 Pooled data for normally-raised and female-raised groups respectively: representing the mean peak correlation values (PCV) for 12 individual males of cross correlations between the distance call at each 4 day interval and the DC before the experiment commenced. It summarises the degree of change of the DC over time in both groups as a whole. Bars shown are standard deviations.

Statistical analyses so far have concentrated on any significant deviations from an individual's DC structure over time in relation to the DC before the experiment began. Cross-correlations were also carried out between an individual's DC and those of its three cagemates to investigate any evidence of convergence to other birds as opposed to individual change. Figures 3.9.1-3.11.6 show the mean PCVs from cross-correlating five examples of the each individuals DC with its cagemates for normally-raised birds: figures 3.9.1-3.9.6 cover all pairwise comparisons for group 1 in experiment 1; figures 3.10.1-3.10.6 for group 2 in experiment 1; and figures 3.11.1-3.11.6 for group 3 in experiment 1. Each graph represents how similar two particular birds were in their DCs at every time interval. The general pattern for all plots in figure 3.15.1 appears to be that there is no obvious sustained trend for normally-raised birds to converge or diverge in the structure of their DCs. Most PCVs fall between 0.62 - 0.72 with some pairs showing remarkably little variation in their level of similarity (e.g. figures 3.10.2, 3.10.4, 3.11.2) and others showing greater fluctuations in the PCVs (e.g. figures 3.9.1, 3.9.6, 3.10.1, 3.11.4).

Bootstrapping was carried out on the PCVs resulting from the inter-individual cross-correlations above. Comparisons were made between consecutive 4 day intervals in a similar manner used to investigate changes over time in individuals. There were no significant differences over time in the level of similarity between normally raised birds ($z<2.58$, $P>0.01$), though some z-scores did approach the level of significance. These fluctuations were however only occasional and do not reflect any marked trend in DC alteration.

The PCVs may at first appear to be quite high (e.g. fig 3.9.2 and fig 3.10.5 showing most data points falling between 0.70-0.75), but when comparing conspecific vocalisations of similar harmonic structure and duration it is usual for most values to be above about 0.60. This is more evident if the figure 3.15.1 are observed in relation to

Fig. 3.9.1 - comparing bird 1 with bird 2

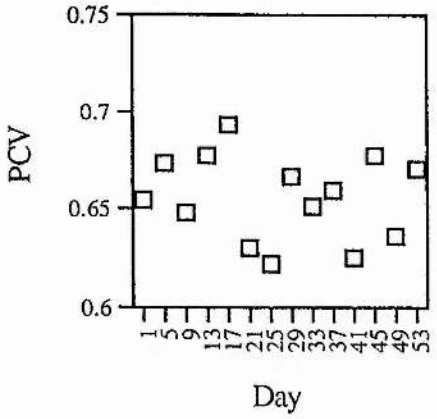


Fig. 3.9.2 - comparing bird 1 with bird 3

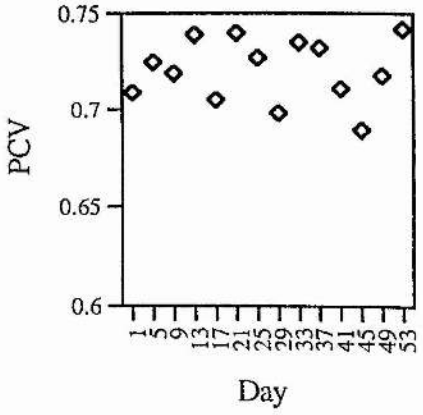


Fig. 3.9.3 - comparing bird 1 with bird 4

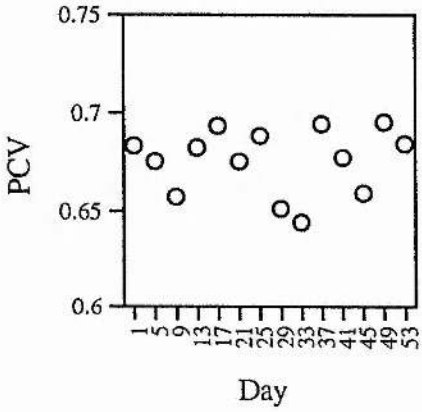


Fig. 3.9.4 - comparing bird 2 with bird 3

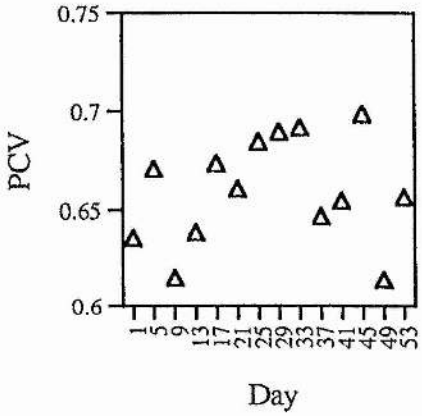


Fig. 3.9.5 - comparing bird 2 with bird 4

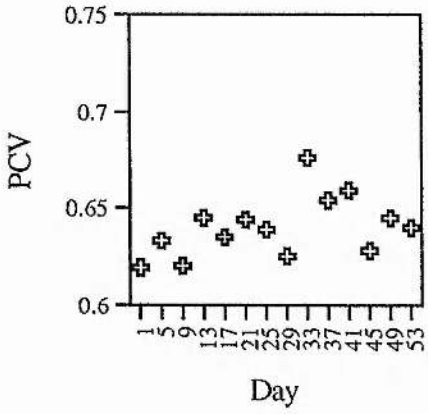


Fig. 3.9.6 - comparing bird 3 with bird 4

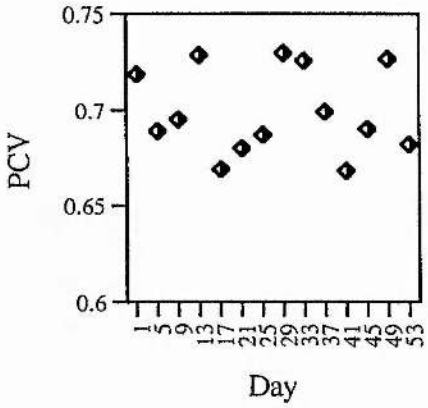


Fig. 3.9.1 - 3.9.6 Normally-raised male zebra finches in group 1, tracing the degree of similarity between two cagemates over time. Each graph represents the peak correlation values (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four birds in group 1.

Fig. 3.10.1 comparing bird 1 with bird 2

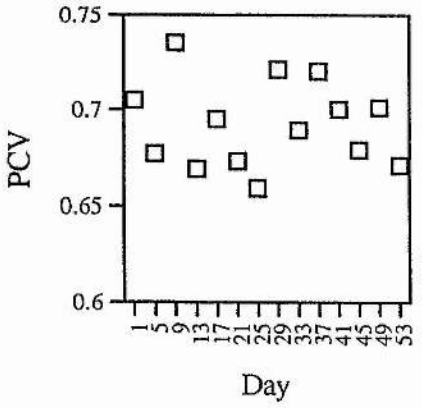


Fig.3.10.2 comparing bird 1 with bird 3

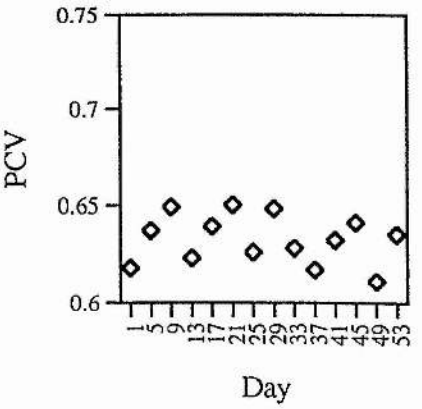


Fig. 3.10.3 comparing bird 1 with bird 4

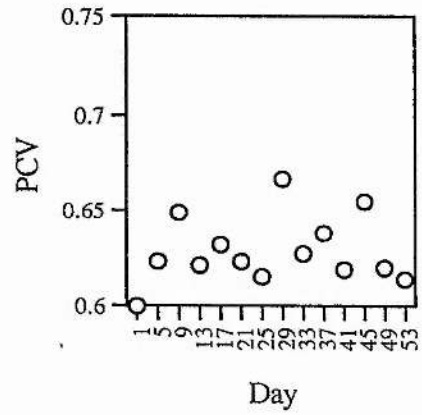


Fig.3.10.4 comparing bird 2 with bird 3

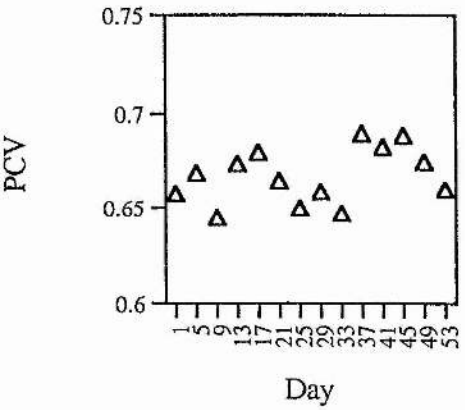


Fig.3.10.5 comparing bird 2 with bird 4

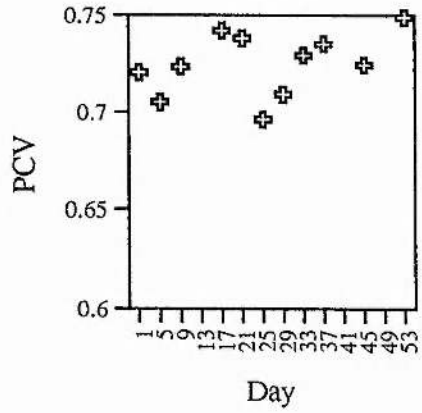


Fig.3.10.6 comparing bird 3 with bird 4

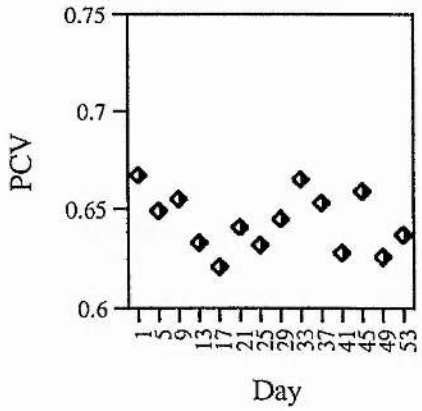


Fig. 3.10.1 - 3.10.6 Normally-raised male zebra finches in group 2, tracing the degree of similarity between two cagemates over time. Each graph represents the peak correlation values (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four birds group 2.

Fig. 3.11.1 comparing bird 1 with bird 2

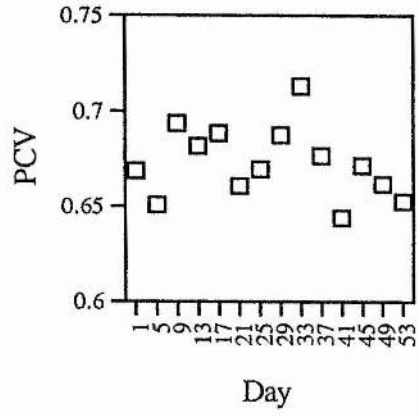


Fig.3.11.2 comparing bird 1 and bird3

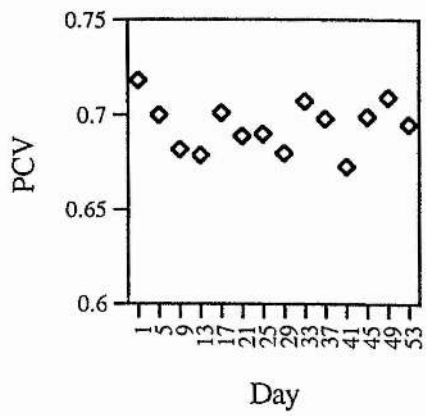


Fig. 3.11.3 comparing bird 1 with bird 4

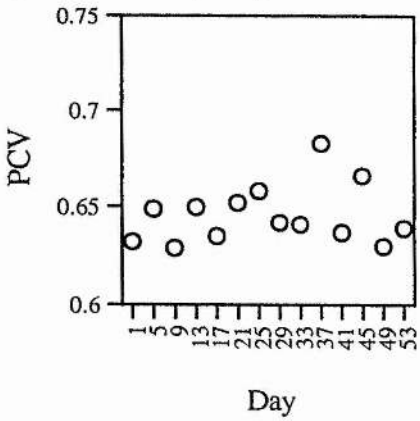


Fig. 3.11.4 comparing bird 2 with bird 3

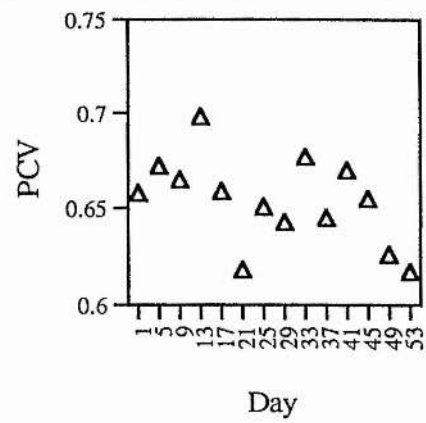


Fig. 3.11.5 comparing bird 2 with bird 4

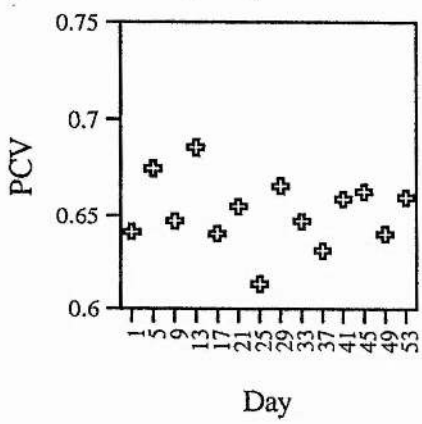


Fig. 3.11.6 comparing bird 3 with bird 4

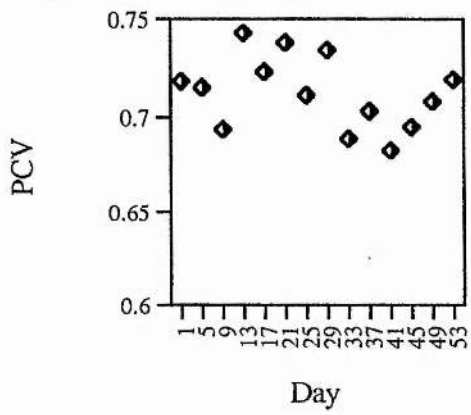


Fig. 3.11.1 - 3.11.6 Normally-raised male zebra finches in group 3, tracing the degree of similarity between two cagemates over time. Each graph represents the peak correlation values (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four birds group 3.

figures 3.2.1-3.4.4 and 3.5.1-3.7.4 representing cross-correlations between DCs within an individuals repertoire sample. In normally-raised birds in particular, the majority of PCVs are above 0.75 with some being as high as 0.85.

Figure 3.12.1-3.14.6 represent similar analyses to figures 3.9.1-3.11.6 but for the female-raised group. Again, there are no obvious trends towards divergence or convergence in the three groups suggesting that the structure of the DC remained relatively unchanged despite notable fluctuations in the PCVs. As a reflection of the greater variation in the DC of female-raised males, the amount of variation in inter-individual comparisons in these birds is also apparently higher than in normally-raised birds in the wider scattering of data points in figure 3.12.1-3.14.6.

For female-raised zebra finches all z-scores obtained from comparisons of the inter-individual comparisons between consecutive recording sessions, are below the value of 2.58 at the 99% confidence limit. This means that there is no significant change in the degree of similarity (or dissimilarity) between cagemates in the female-raised treatment groups; in other words, no convergence had occurred. This is most clearly observed in figures 3.15.1 and 3.15.2 for normal and female-raised birds respectively, which represents the mean plots of both populations. There is no obvious change in the mean PCV from these graphs.

The inter-individual comparison data for both experimental treatment groups which is presented in figures 3.9.1-3.11.6 and 3.12.1-3.14.6 were themselves compared by bootstrapping. A z-score of 1.13 ($P>0.01$) was obtained from this procedure, indicating that there is a no significant difference in the degree of similarity amongst individuals between normal-raised and female-raised zebra finches. Males that were female-raised are not more different to one another in the structure of their DCs than normal-raised males.

Fig. 3.12.1 comparing bird 1 with bird 2

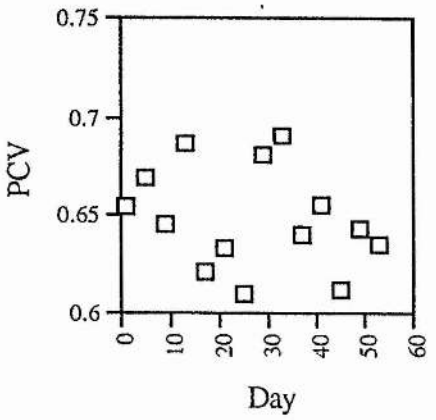


Fig. 3.12.2 comparing bird 1 with bird 3

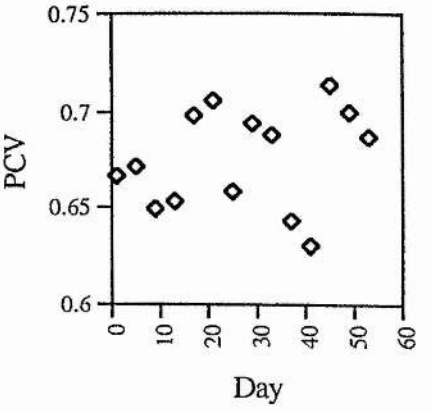


Fig. 3.12.3 comparing bird 1 with bird 4

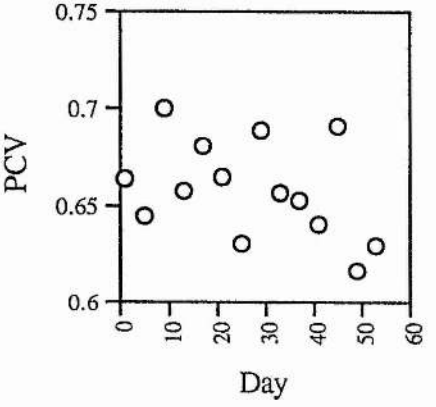


Fig. 3.12.4 comparing bird 2 with bird 3

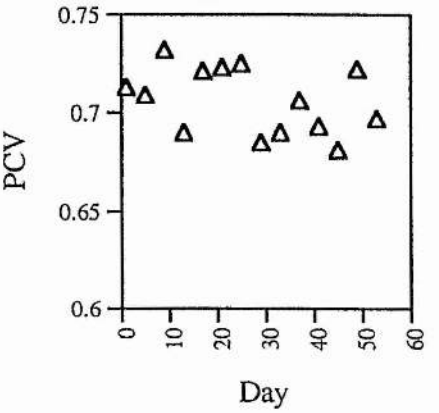


Fig. 3.12.5 comparing bird 2 with bird 4

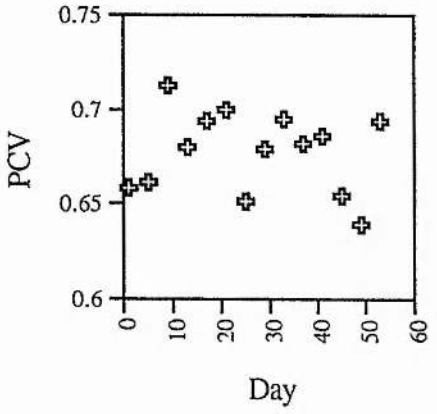


Fig. 3.12.6 comparing bird 3 with bird 4

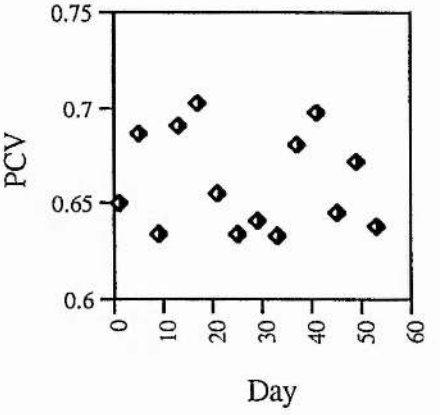


Fig. 3.12.1 - 3.12.6 Female-raised male zebra finches in group 1, tracing the degree of similarity between two cagemates over time. Each graph represents the peak correlation value (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four birds in group 1.

Fig. 3.13.1 comparing bird 1 with bird 2

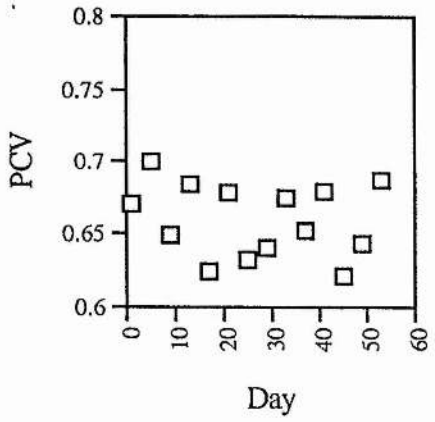


Fig. 3.13.2 comparing bird 1 with bird 3

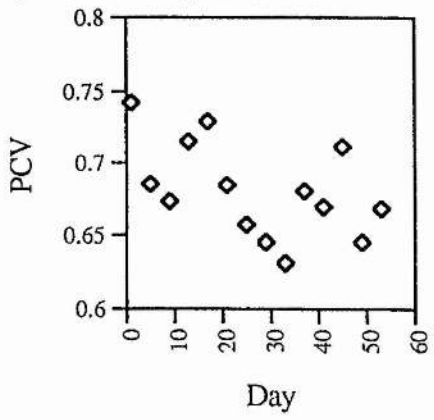


Fig. 3.13.3 comparing bird 1 with bird 4

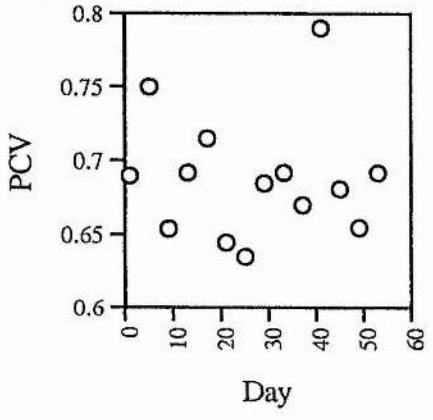


Fig. 3.13.4 comparing bird 2 with bird 3

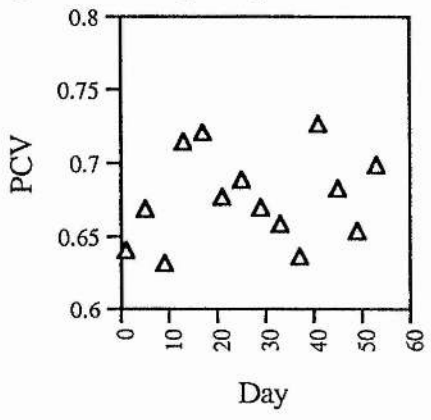


Fig. 3.13.5 comparing bird 2 with bird 4

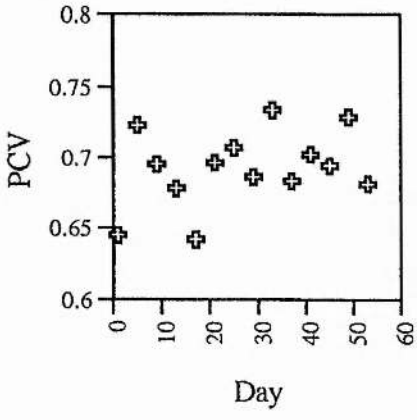


Fig. 3.13.6 comparing bird 3 with bird 4

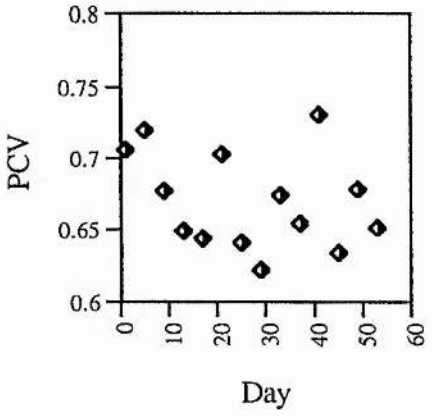


Fig. 3.13.1 - 3.13.6 Female-raised male zebra finches in group 2, tracing the degree of similarity between two cagemates over time. Each graph represents the peak correlation value (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four birds in group 2.

Fig. 3.14.1 comparing bird 1 with bird 2

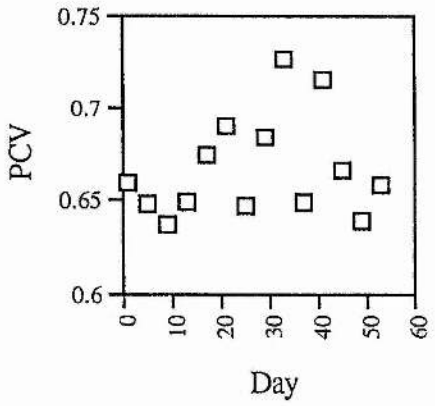


Fig. 3.14.2 comparing bird 1 with bird 3

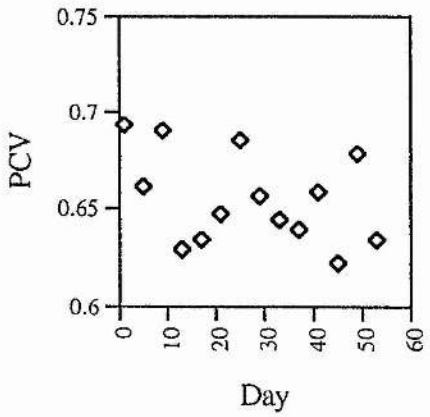


Fig. 3.14.3 comparing bird 1 with bird 4

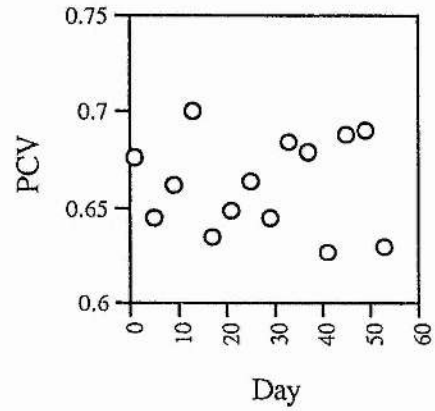


Fig. 3.14.4 comparing bird 2 with bird 3

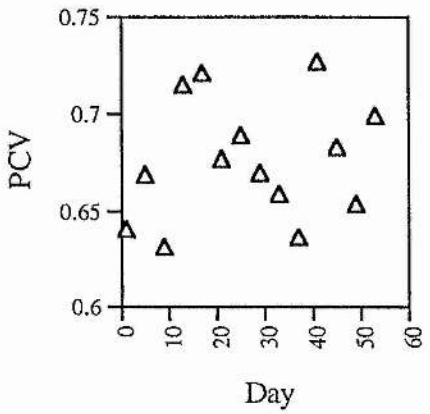


Fig. 3.14.5 comparing bird 2 with bird 4

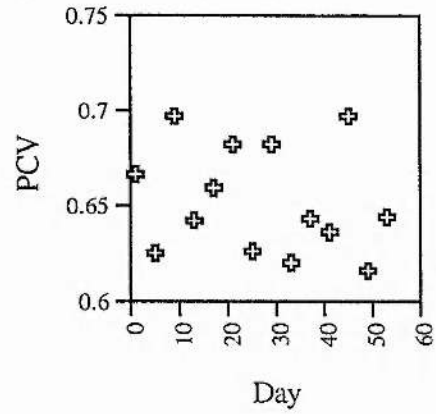


Fig. 3.14.6 comparing bird 3 with bird 4

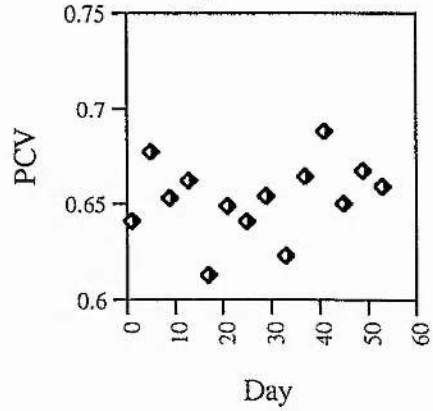


Fig. 3.14.1 - 3.14.6 Female-raised male zebra finches in group 3, tracing the degree of similarity between two cagemates over time. Each graph represents the peak correlation value (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four birds in group 3.

Fig. 3.15.1 for normal-raised birds

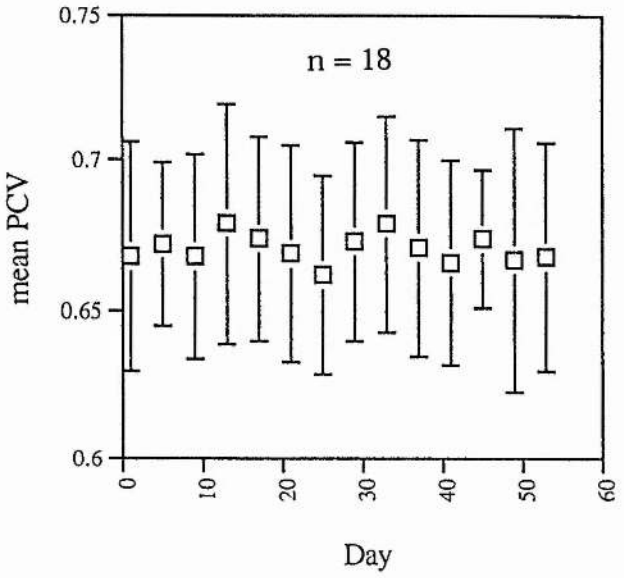


Fig. 3.15.2 for female-raised birds

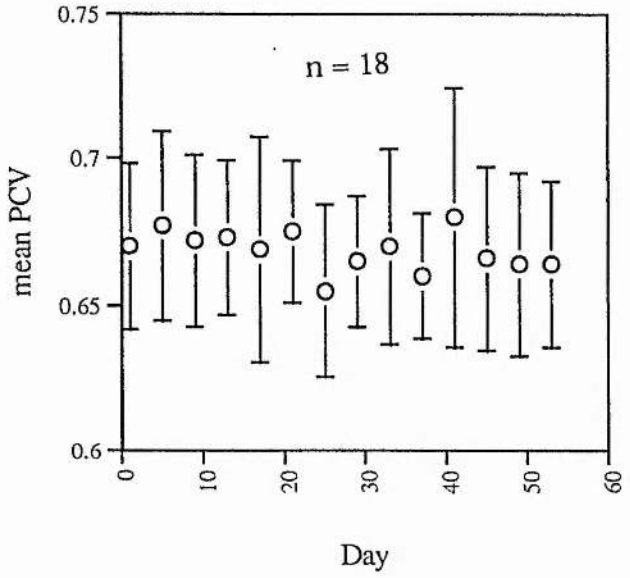


Fig. 3.15.1 - 3.15.2 The mean PCV of graphs 3.9.1-3.11.6 for normal-raised and graphs 3.12.1-3.14.6 for female-raised respectively. The PCV are the result of cross-correlation comparisons between the DC of two individuals, pooled for all possible pairwise comparisons in each treatment group.

Figures 3.16.1-3.18.6 traces the inter-individual similarity of the DC in the female-raised subjects of experiment 3. Again, from the graphs there is no evidence of either call convergence or divergence in this treatment group There is no suggestion of a decrease or increase in the similarity between individuals from the PCVs in figure 3.19, which illustrates the results of the three groups in experiment 3 as a whole. All values from bootstrap comparisons for pairs between 4 day intervals were below the threshold value of 2.58 ($P<0.01$) which indicates no significant difference.

Although the results of inter-individual comparisons of young zebra finches in experiment 3 reveal that there was no tendency for any change in similarity between cagemates, and therefore no evidence of convergence or divergence, it was necessary to test whether these birds had converged at all to the DC of the tutor. There is the possibility that all individuals changed their call in accordance with the normal adult male tutor model, in a synchronous fashion, in which case there would not be a noticeable change between experimental subjects, as was observed. Figures 3.20.1-3.22.4 show the PCVs resulting from comparisons of each individual's DC with that of the tutor over the duration of the study. The level of similarity appears to remain relatively stable between young abnormal zebra finches and the normal tutor (see figure 3.23 for the group as a whole), suggesting that even this salient stimulus does not cause an extension in vocal plasticity. Bootstrapping comparisons between tutors and potential tutees revealed that none of the comparisons were statistically significant; there was no difference between 4 day intervals in terms of the PCV or degree of similarity.

Sonagrams of the calls of all individuals in the three experimental treatments are shown in Figures 24, 25 and 26 for normally-raised, female-raised and female-raised with normal adult tutor groups. The sonagrams show visually that there was no significant change in the basic structure of the distance call between week 1 and week 8, despite small variations in parameters such as the duration. In Figures 25 and 26 it can be seen

Fig. 3.16.1 comparing bird 1 with bird 2

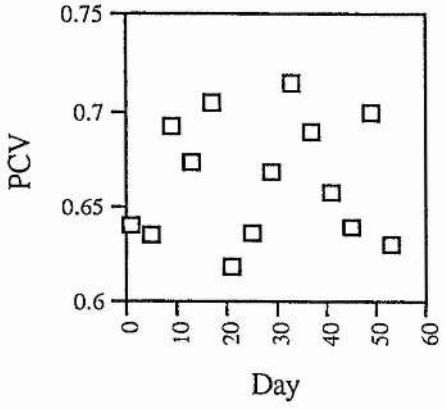


Fig. 3.16.2 comparing bird 1 with bird 3

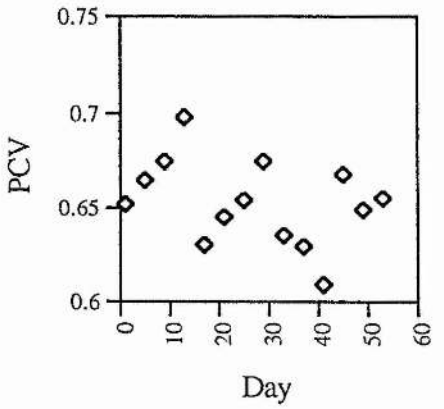


Fig. 3.16.3 comparing bird 1 with bird 4

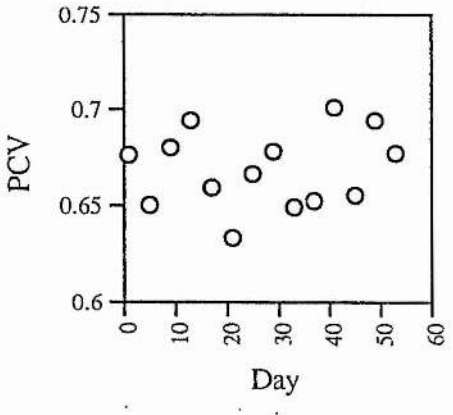


Fig. 3.16.4 comparing bird 2 with bird 3

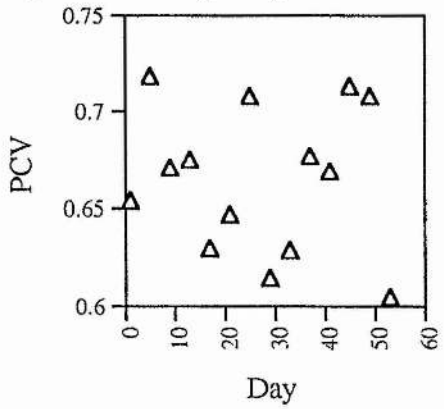


Fig. 3.16.5 comparing bird 2 with 4

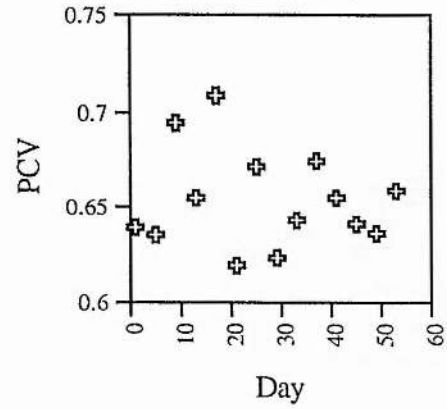


Fig.3.16.6 comparing bird 3 with bird 4

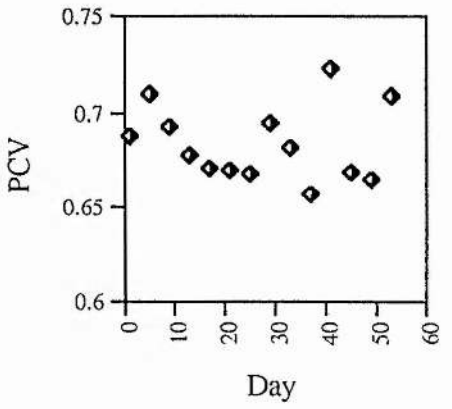


Fig. 3.16.1 - 3.16.6 The degree of similarity between two cagemates over time for female-raised male zebra finches presented with a suitable male tutor in adulthood. Each graph represents the peak correlation value (PCV) resulting form cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four experimental subjects in group 1.

Fig. 3.17.1 comparing bird 1 with bird 2

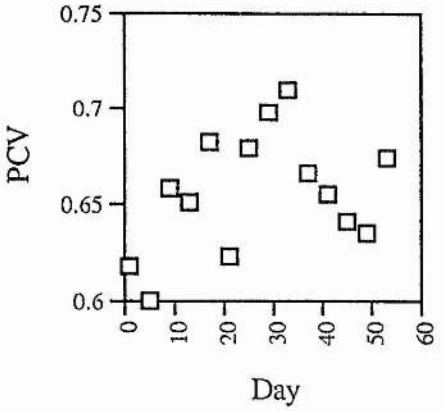


Fig.3.17.2 comparing bird 1 with bird 3

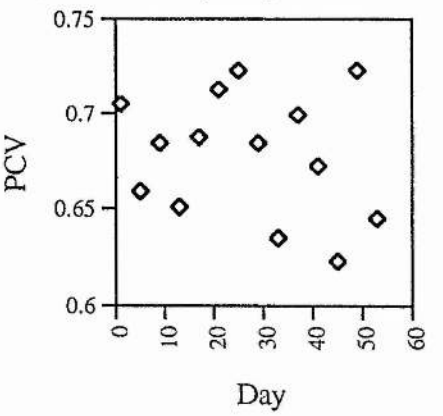


Fig.3.17.3 comparing bird 1 with bird 4

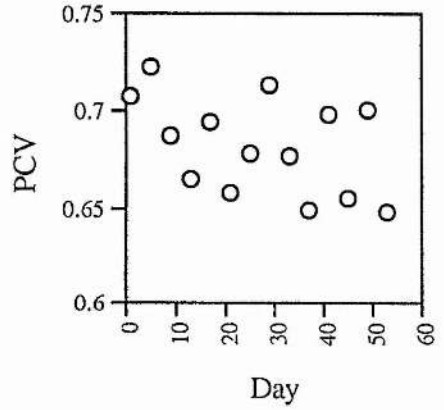


Fig.3.17.4 comparing bird 2 with bird 3

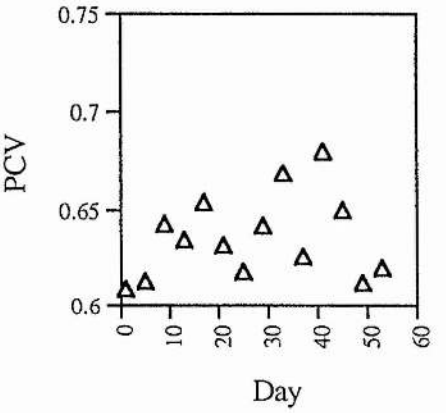


Fig. 3.17.5 comparing bird 2 with bird 4

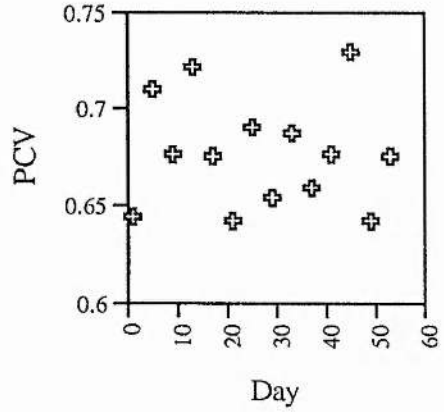


Fig. 3.17.6 comparing bird 3 with bird 4

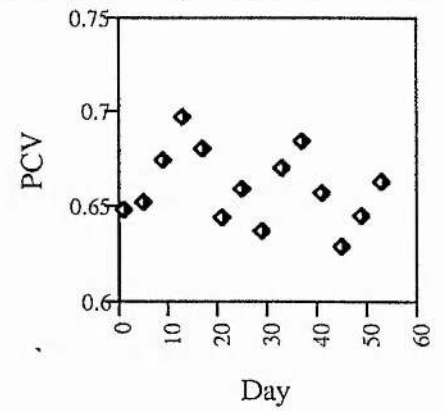


Fig. 3.17.1 - 3.17.6 The degree of similarity between two cagemates over time for female-raised male zebra finches presented with a suitable male tutor in adulthood. Each graph represents the peak correlation value (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four experimental subjects in group 2.

Fig. 3.18.1 comparing bird 1 with bird 2

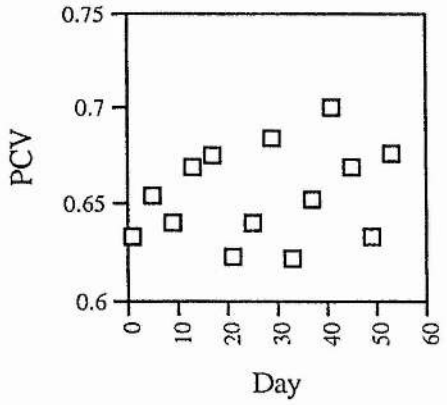


Fig. 3.18.2 comparing bird 1 with bird 3

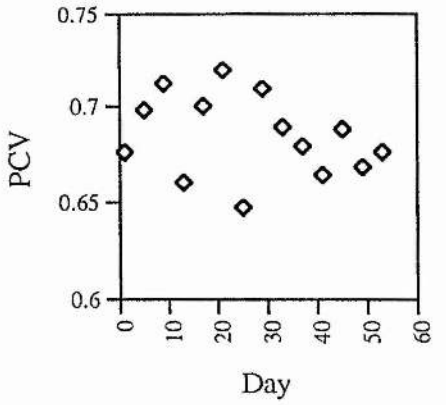


Fig. 3.18.3 comparing bird 1 with bird 4

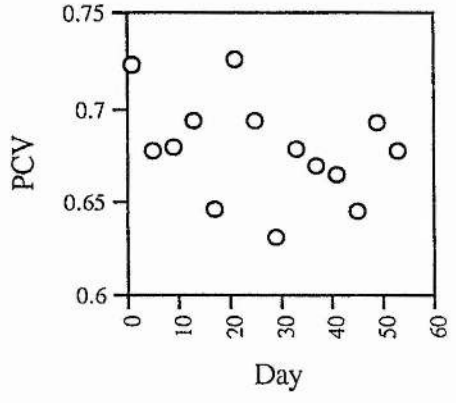


Fig. 3.18.4 comparing bird 2 with bird 3

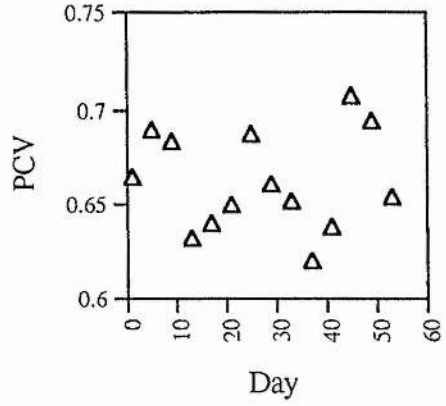


Fig. 3.18.5 comparing bird 2 with 4

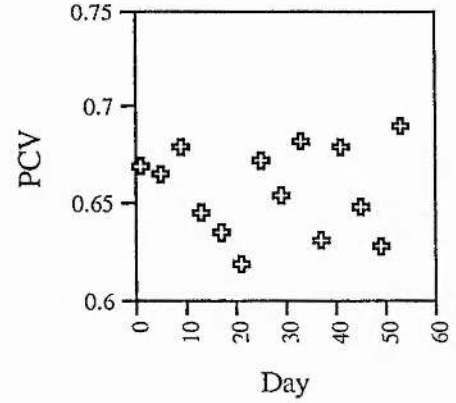


Fig. 3.18.6 comparing bird 3 with bird 4

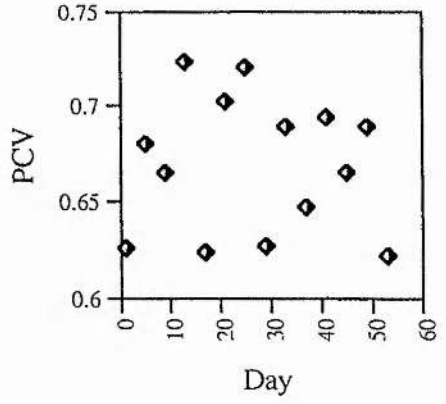


Fig. 3.18.1. - 3.18.6 The degree of similarity between two cagemates over time for female-raised male zebra finches presented with a suitable male tutor in adulthood. Each graph represents the peak correlation value (PCV) resulting from cross-correlations of distance calls between two birds. The six graphs together show all possible pairwise comparisons between all four experimental subjects in group 3.

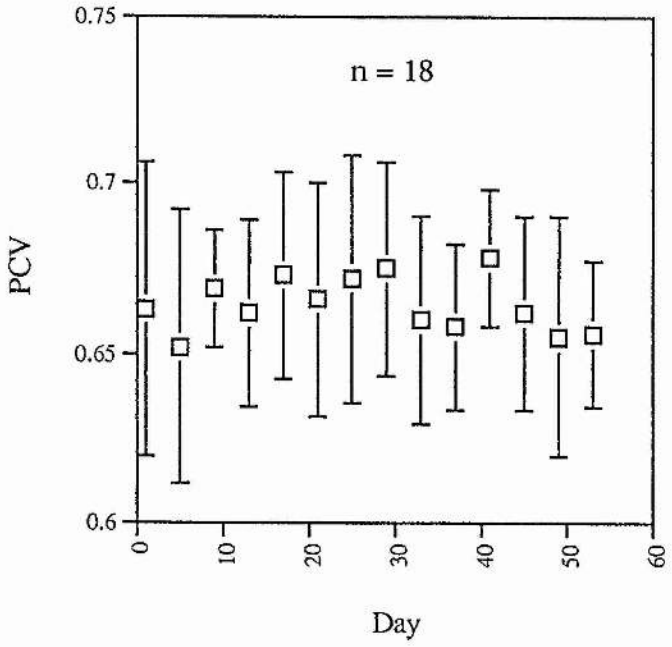


Fig. 3.19 The mean peak correlation value (PCV) of female-raised birds represented in Fig. 3.16.1-3.18.6. The PCVs are the result of cross-correlation comparisons between pairs of individuals with the mean values calculated from the pooled sample of all pairwise comparisons.

Fig.3.20.1 comparing tutor with bird 1

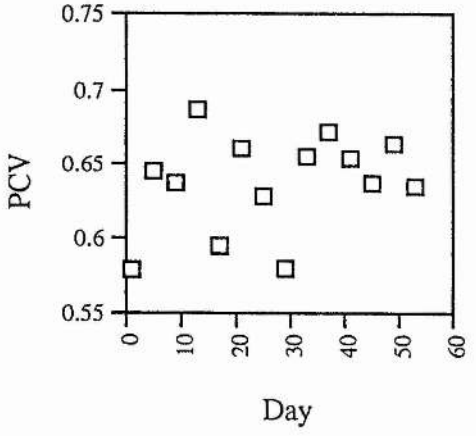


Fig. 3.20.2 comparing tutor with bird 2

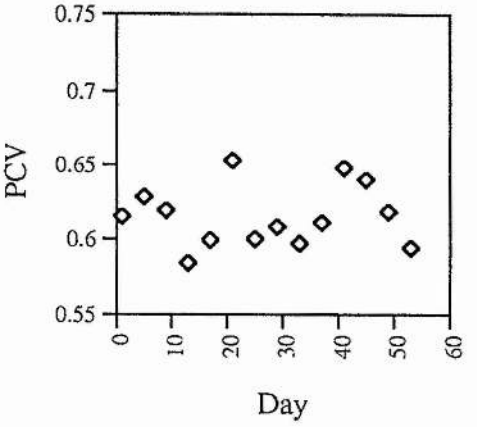


Fig. 3.20.3 comparing tutor with bird 3

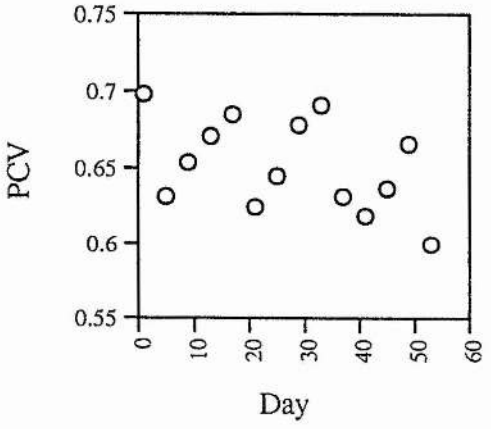


Fig. 3.20.4. comparing tutor with bird 4

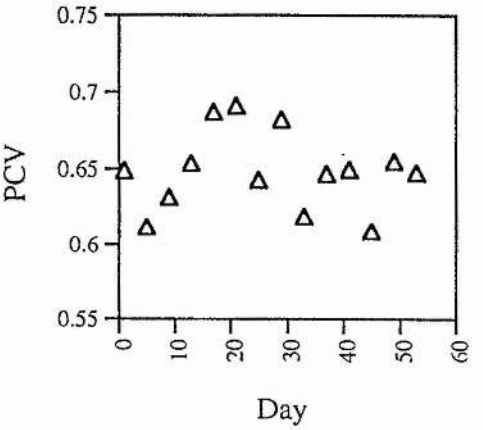


Fig. 3.20.1 - 3.20.4 Peak correlation values (PCV) for each 4 day interval from comparisons of the DC between female-raised zebra finches and normal tutors. Each graph traces the changes in the DC for each individual in group 1.

Fig. 3.21.1 comparing tutor with bird 1

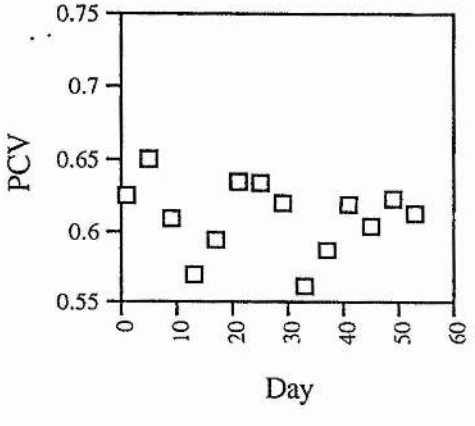


Fig. 3.21.2 comparing tutor with bird 2

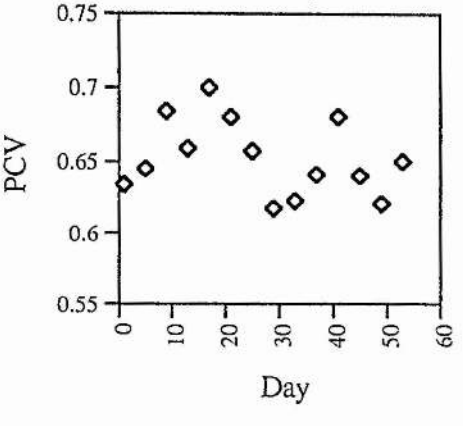


Fig. 3.21.3 comparing tutor with bird 3

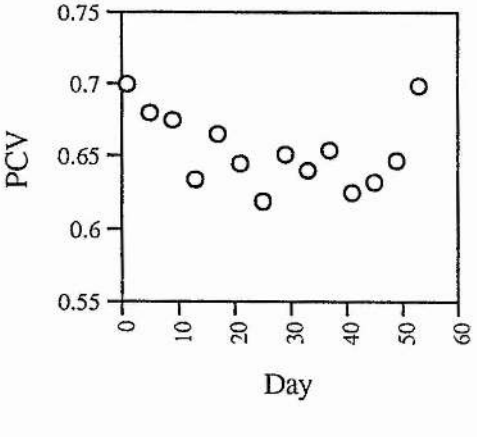


Fig.3.21.4 comparing tutor with bird 4

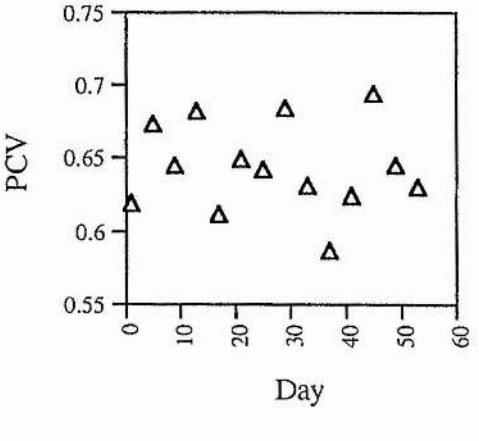


Fig. 3.21.1 - 3.21.4 Peak correlation values (PCV) for each 4 day interval from comparisons of the DC between female-raised zebra finches and normal tutors. Each graph traces the changes in the DC for each individual in group 2.

Fig. 3.22.1 comparing tutor with bird 1

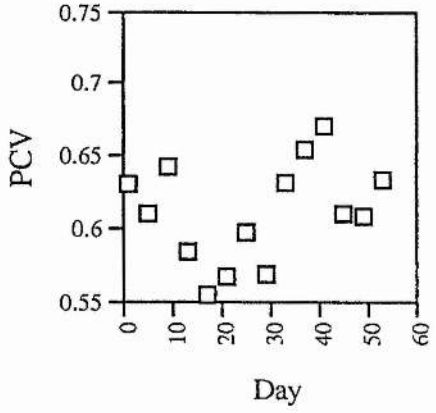


Fig. 3.22.2 comparing tutor with bird 2

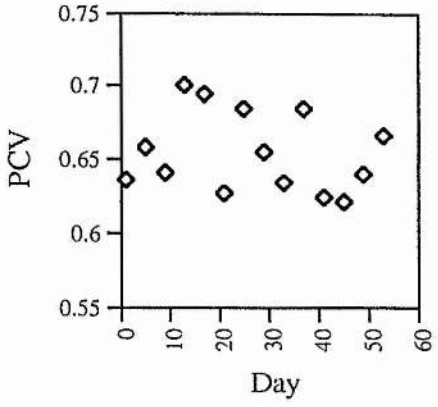


Fig. 3.22.3 comparing tutor with bird 3

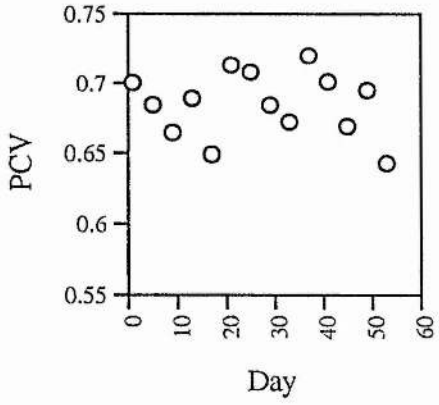


Fig. 3.22.4 comparing tutor with bird 4

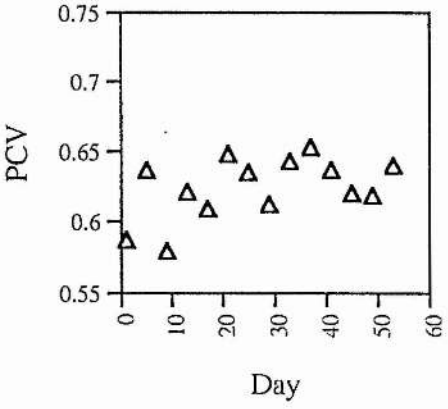


Fig.3.22.1 - 3.22.4 Peak correlation values (PCV) for each 4 day interval from comparisons of the DC between female-raised zebra finches and normal tutors. Each graph traces the changes in the DC for each individual in group 3.

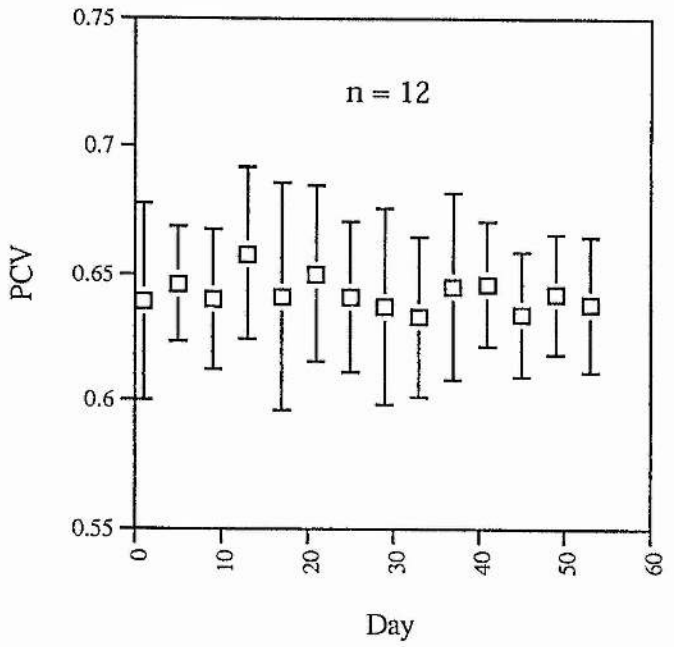


Fig.3.23 The mean pooled data from graphs 3.20.1-3.22.4. The peak correlation values (PCV) are the result of cross-correlation comparisons between each of the 12 female-raised individuals DCs and that of the normal adult male tutor for each group.

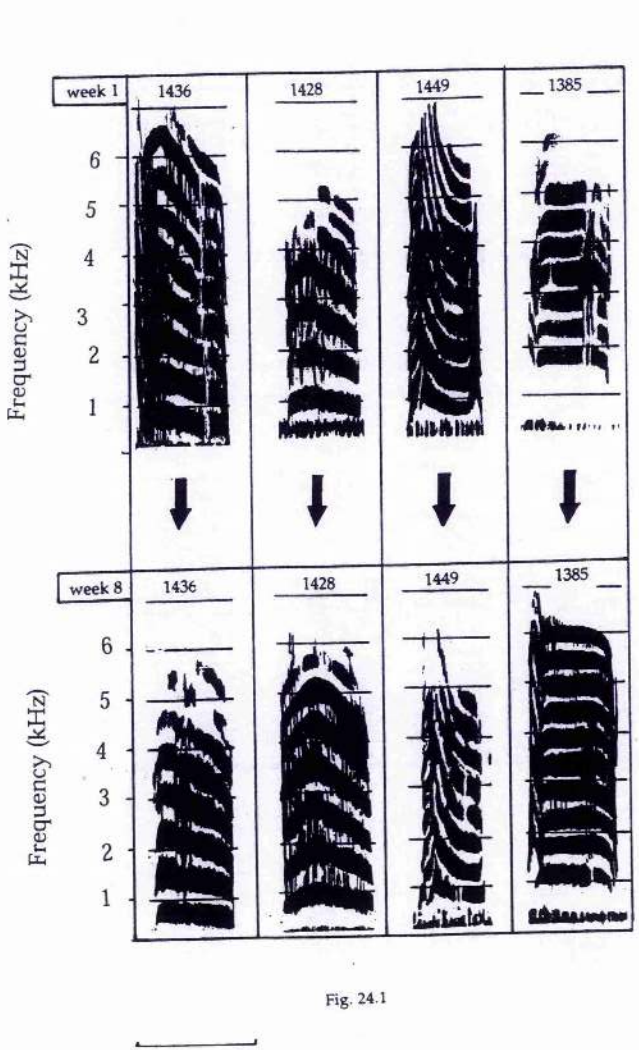


Fig. 24.1

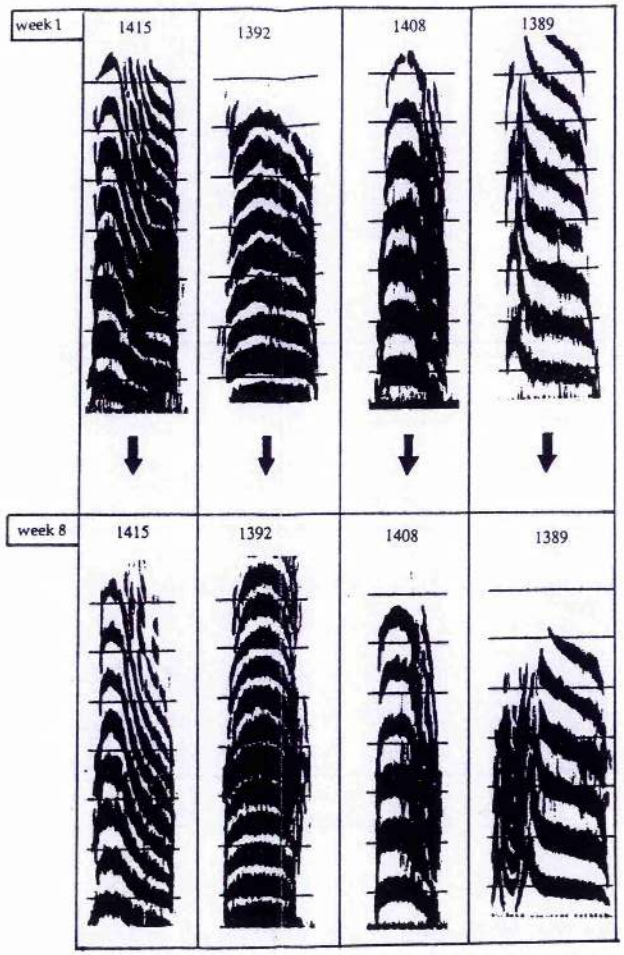


Fig. 24.2

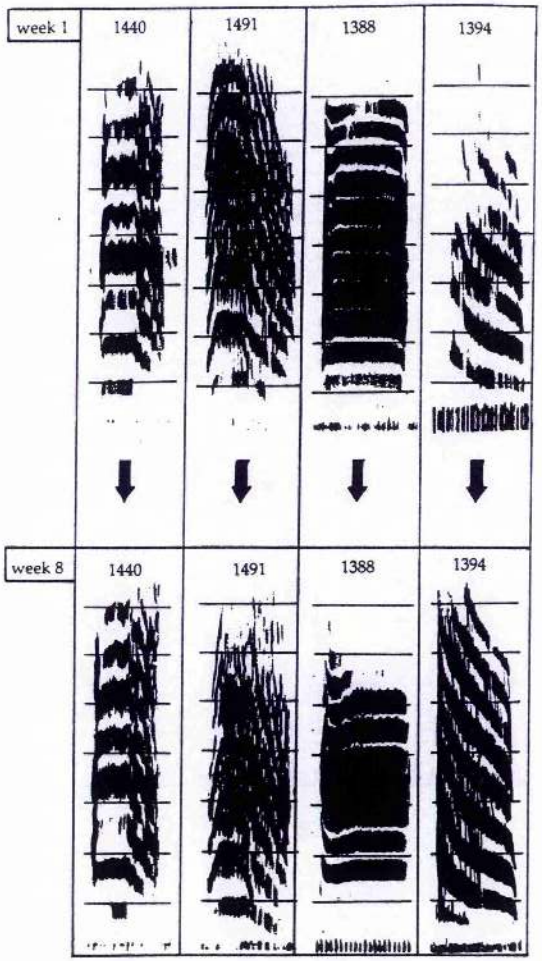


Fig. 24.3

Figure 24. Sonagrams of the distance calls of normally-raised zebra finch males in week 1 and week 8 of the study. Fig. 24.1, 24.2 and 24.3 represent the calls of individuals in groups 1, 2 and 3 respectively.

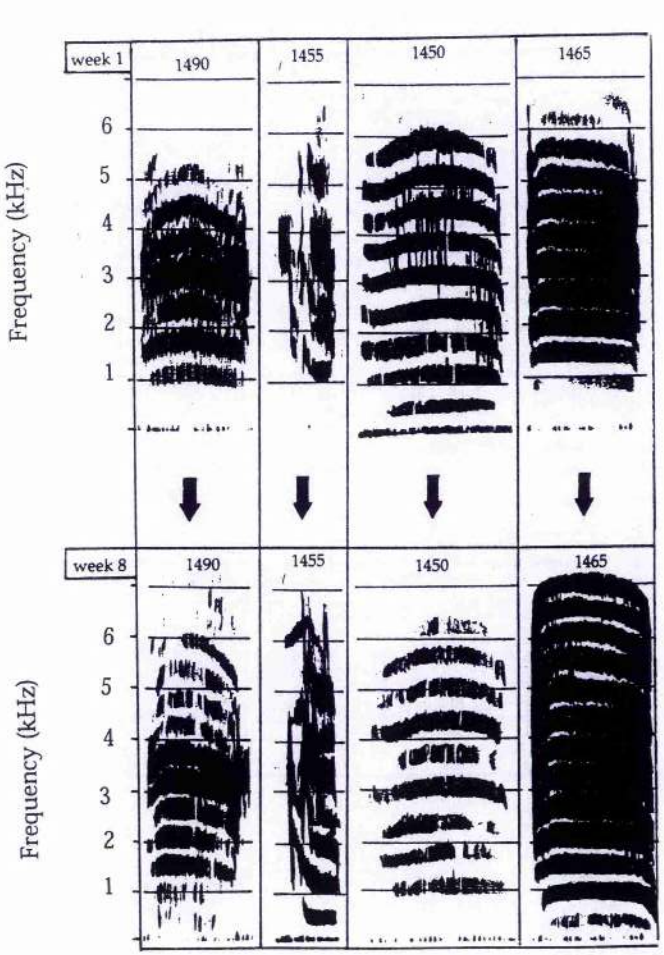


Fig. 25.1

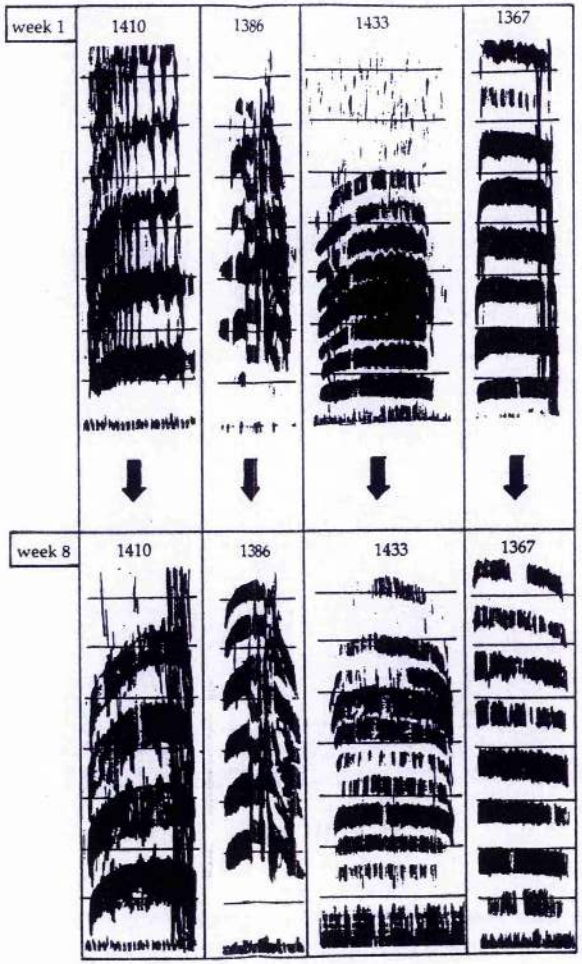


Fig. 25.2

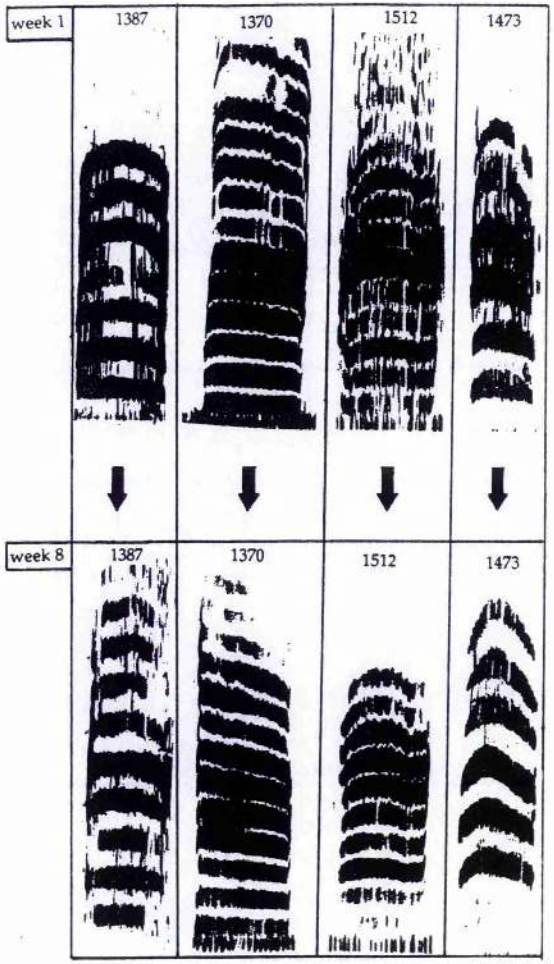


Fig. 25.3

Figure 25. Sonagrams of the distance calls of female-raised zebra finch males in week 1 and week 8 of the study. Fig. 25.1, 25.2 and 25.3 represent the calls of individuals in groups 1, 2 and 3 respectively.

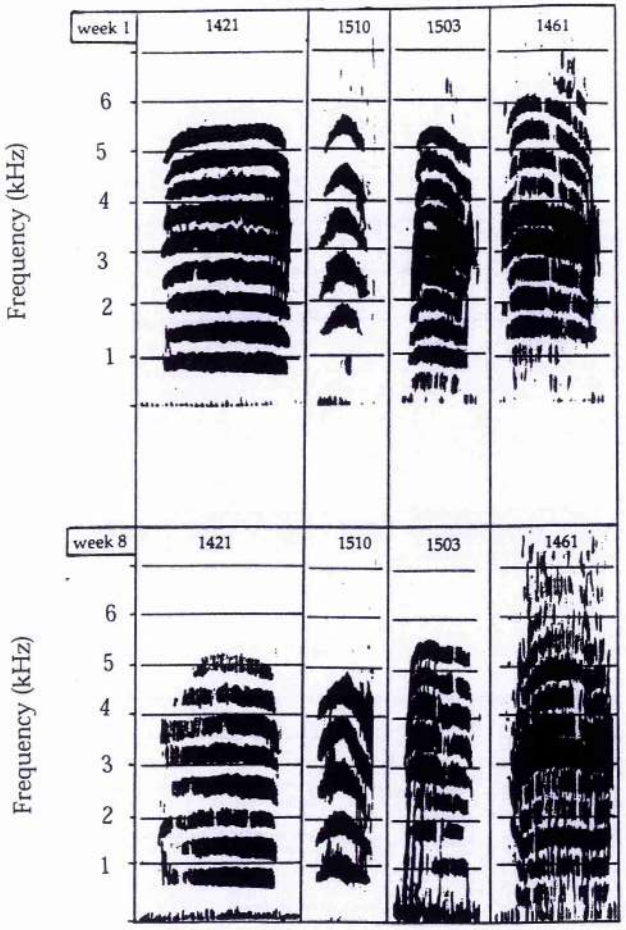


Fig. 26.1

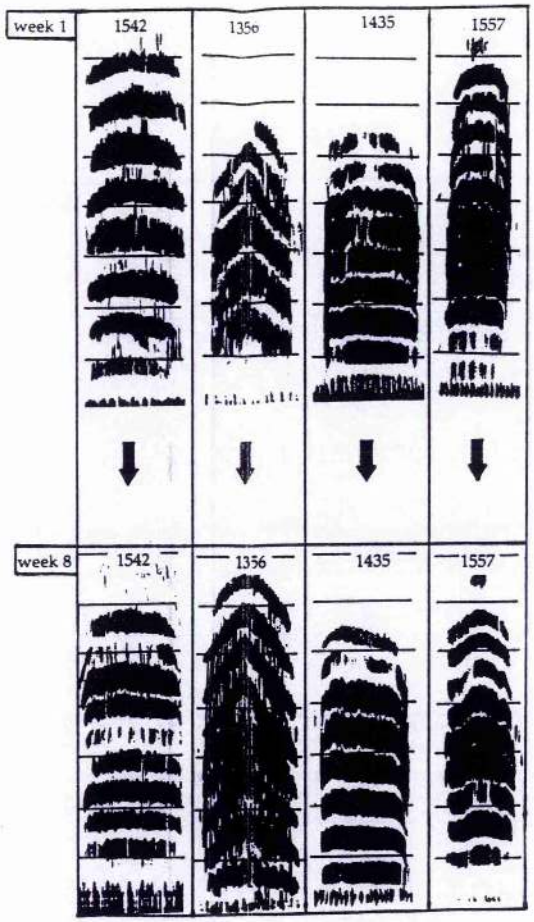


Fig. 26.2

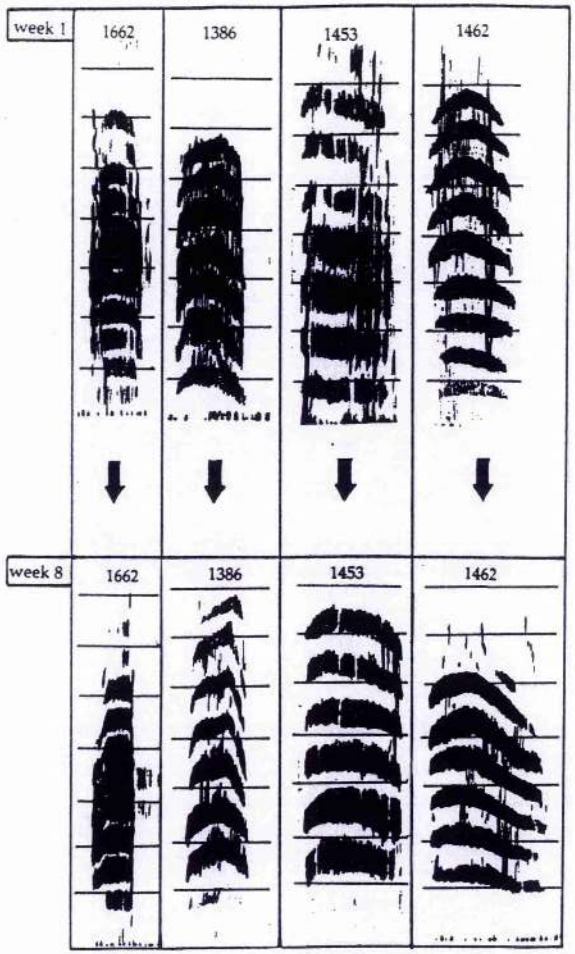


Fig. 26.3

0.5 sec.

Figure 26. Sonagrams of the distance calls of female-raised zebra finch males that were provided with a normal male tutor, in week 1 and week 8 of the study. Fig. 26.1, 26.2 and 26.3 represent the calls of individuals in groups 1, 2 and 3 respectively.

that the young males that were female-raised have typically female calls which are generally longer in duration and which lack the noise element of adult male calls (see fig. 24).

3.4. Discussion

Zebra finches have been shown to learn their vocalisations early in their development during a sensitive phase, after which the potential for acquiring new elements, songs or calls is heavily restricted. Some studies have been able to define the timing of the sensitive phases relatively accurately (Eales, 1985, 1987; Clayton, 1987; Slater *et al.*, 1988; Böhner, 1990), so that now song learning is generally accepted to occur in the period 35-70 days, provided an appropriate conspecific adult male is provided as a model tutor. However, the process of song acquisition is not strictly confined to this period of 35 or so days.

Clayton (1987) found that if a young zebra finch is provided with a tutor of a different species, then the song of the father heard before 35 days of age tends to be reproduced. Denial of any tutor model, including non-conspecifics, during the sensitive phase, produces a similar result (Böhner, 1990). Eales (1985, 1987) subjected the young males in her experiments to similar deprivation and found that they produced abnormal songs. These zebra finches could, however, change their songs after 65 days of age if they were provided with singing adult male zebra finches, although Slater *et al.* (1993) caution on whether these birds were modelling themselves on the tutors after 65 days or altering their songs in some other way.

The possibility of finding that age-dependent learner species have the potential for vocal plasticity in adulthood has encouraged many further studies on song learning and was the motivation for the present study. Both songs and calls are learnt, at least in part, in

zebra finches, and this learning involves acquisition during sensitive phases; for song this has been shown to occur at between 35-65 days of age, whereas for calls it is earlier in the development of the bird during the nestling and fledgling stage at between 15 to 35 days (Jones, 1994).

Zann (1985) cross-fostered young zebra finches to Bengalese finches to investigate the effects that this would have on the learning of the distance call (DC). Zebra finch males appear to inherit fairly detailed species-specific specifications on the frequency of maximum amplitude (FMA) of the DC, the fundamental frequency (FF), the number of harmonics and details on the duration of the call. His results suggested that the template for the acquisition of the normal DC of zebra finches is open to certain environmental influences in males but not females. Most males appear to inherit specifications on the noise element of the DC (the most sexually diagnostic feature of the call) but an appropriate model is needed for normal modulation to occur after day 40. It is evident from Zann's study that certain sexually dimorphic characteristics of the male DC, notably the noise element, are acquired later in development. This raises the question of how long young birds can extend their ability to modify their calls and whether early experience can affect call plasticity as it appears to in song learning?

The results of the present study provide no indication that vocal plasticity is present in the distance call of zebra finches in adulthood. All the young males involved in the three experiments were placed in close proximity with other males of similar experience. It is known that social factors are important in the learning of vocalisations (Baptista & Petrinovich, 1984, 1986; Clayton, 1988; Slater *et al.,* 1988; Eales, 1989; Mann, 1991) and therefore it was assumed that incorporation of a strong social influence into the experimental protocol would be likely to result in call convergence should the birds possess such a potential.

The first experiment acted as a control for experiments 2 and 3, in which young birds were manipulated to limit their social experience from hatching. In experiment 1, young males that had been raised by both parents and acquired a normal male DC, were placed together with other normal-raised males at 120 days. The results of cross-correlations between these birds on an intra- and inter-individual level showed that there was neither any divergence in an individual's sample of DCs from the start to the finish of the eight weeks of the study, nor any convergence in the DCs of cagemates. This is probably not surprising considering that the young birds did receive suitable auditory stimulation from their father from hatching until independence, and the distance call had therefore been acquired and become 'fixed' under somewhat optimal conditions. In normal-raised adult male zebra finches the distance call is highly stable and the potential for vocal plasticity is very unlikely.

There does appear to be a notable degree of variation between successive weeks from looking at the graphical representations of the data, but these slight changes in the peak correlation values (PCV) from the comparisons of two calls are neither significant nor sustained, and probably an artefact of recording variations. Since cross-correlation analysis appears to be fairly sensitive to changes and no two distance calls uttered by the same bird are 100% similar, there will appear to be fluctuations over time in the DC. These fluctuations are evidently more pronounced in female-raised birds as shown by the higher variance in the mean PCV of the group as a whole. From inspection of the sonagrams of these recordings it appears that the duration of the call varies most and would be likely to cause this affect. Female-raised males possess an abnormal DC in that the noise element is missing and the call is more female-like due to its limited frequency modulation. The DC in these birds appears to be less stereotyped, which may suggest that it would be more prone to change in adulthood.

Female-raised zebra finches had experienced a very different environment from their normal-raised counterparts. They had not been exposed to any adult male conspecifics

at any stage; the only auditory stimuli received were those of their mother and siblings. Even under this highly inadequate background, there was no evidence in this study of any tendency to change the calls in adulthood by converging with their cagemates. All cagemates were however, similarly raised and all abnormal in terms of their individual vocalisations. It is therefore conceivable that despite their deprived upbringing, and the imposed confines of close proximity with other conspecifics, there needs to be some other salient factor which will prolong learning into adulthood.

Baptista & Petrinovich (1986) succeeded in demonstrating song learning in white-crowned sparrows (*Zonotrichia leucophrys*) after 50 days where Marler (1970) had failed, by using live tutors instead of tape recordings. The presence of a live conspecific male zebra finch tutor in a close social group with socially deprived young adults represents a very salient stimulus and probably the most likely environment in which to observe vocal plasticity. This was the rationale behind the protocol of the third experiment in which female-raised males were housed with three cagemates of similar experience with the addition of a normal adult male tutor.

The results of experiment 3 seem to mirror those of experiments 1 and 2. Despite the seemingly ideal conditions for vocal plasticity there was no indication that any of the subjects had copied the tutor, or indeed modified their calls at all. Whereas previously, the normal conditions of development in experiment 1 or the lack of any appropriate tutor to model the DC from in experiment 2 were possible reasons for the lack of any vocal plasticity, the most obvious conclusion that can be drawn from experiment 3 was that zebra finches cannot modify their calls after they have acquired them early in their development. Vocal plasticity may be possible in the process of song learning but not apparently in call note learning.

It is possible that the length of the study period of eight weeks was not enough time for the process of call modification to occur, either through call convergence by mutual

imitation of cagemates as in black-capped chickadees (Mammen, 1981) or by direct copying of an appropriate tutor. This is unlikely for several possible reasons. Firstly, one would expect some kind of sustained change, however slight, to manifest itself after eight weeks. Despite the fluctuations in the peak correlation values between successive recording sessions, a maintained change in the DC is not observed for any of the 36 individuals involved in the three experiments. Secondly, one might expect that age-dependent learners could not extend their sensitive phase for learning indefinitely, and therefore the likelihood of a call becoming fixed in an individual would increase with age. If a change were to occur it is reasonable to assume that it would do so sooner rather than later in adulthood.

As the process of call learning and song learning are thought to be distinctive and separate in occurrence (Jones, 1994), one should perhaps heed caution in generalising the results of studies from one to the other. The sensitive phase for call learning commences prior to that for song learning but there is a degree of overlap between the two (Slater & Jones, 1995). Zann (1985) describes it as ending before 40 days, which means that the young are predisposed to learn the DC from their father. The level of similarity in the DC between fathers and sons is significantly high (Zann, 1985, 1990) and the DC should reflect kinship in the colony. If conspecifics were to use DCs as reliable cues in kin recognition then the call would have to be fairly robust and resistant to change.

CHAPTER 4

CAN BUDGERIGARS LEARN NEW CALLS IN THE ABSENCE OF SOCIAL FACTORS ?

4.1. Introduction

Call learning is known to occur in at least two orders of birds for which vocal learning is common: the Passeriformes (perching birds; Mundinger, 1979) and the Psittaciformes (parrots; Rowley, 1980; Rowley & Chapman, 1986), and it is known to be widespread in at least one taxon, the cardueline finches (Güttinger, 1974; Marler & Mundinger, 1975). Call learning in the carduelines may not be restricted to particular sensitive phases and, in at least some age-independent learners, new calls can be acquired in adulthood (e.g. Mammen & Nowicki, 1981; Marler & Mundinger, 1975).

Chapter 3 described how there was no evidence for vocal plasticity in the distance call of adult zebra finches, despite a suggestion of their ability to learn new song elements by an earlier study (Slater *et. al.,* 1993). The stability of the distance call remained throughout adulthood, even in birds that had experienced extreme social deprivation during their development and not been exposed to appropriate male models.

Studies on other passeriform species have shown that social interaction facilitates call learning, and that retention of vocal plasticity seems to be related to changes in an animal's social environment. Black-capped chickadees will converge in the structural details of their calls if housed together with unfamiliar birds (Mammen & Nowicki, 1981; Mundinger, 1979), and even closely related species have been shown to converge (e.g pine siskins, *Carduelis spinus*, housed with European siskins, *C. spinus;* Mundinger, 1970, 1979). In this last study, Mundinger (1979) describes how the birds that interacted least in his experimental group did not imitate each other.

Psittaciformes (parrots) are an order of birds in which learning of vocalisations is widespread and open-ended (Rowley & Chapman, 1986). Some species (e.g. cockatoo, *Cacatua roseicapilla*) form large highly social groups and have flock specific calls, in which all members of the group share a common call (e.g. budgerigar, *Melopsittacus undulatus*). The distance or contact call is the most frequently uttered sound in the budgerigars' vocal repertoire (Brockway, 1969) and is used when a bird is separated from conspecifics, during flight, or when preparing to roost for the night (Wyndham, 1980). The contact call of the budgerigar can also be incorporated into the warble song (Farabaugh *et. al.,* 1994), rather like the distance call of the zebra finch.

Contact calls are known to be learnt in budgerigars: rearing young birds in acoustic isolation (Dooling *et. al.,* 1987b) and deafening of nestlings both result in the production of an abnormal call (Dooling *et. al.,* 1987a). Learning in this species is not, however, restricted to a sensitive phase early in development. Brown *et. al.* (1988) observed that if unfamiliar budgerigars are kept together in the same cage, their calls converge to a group specific call, which is distinct from other groups housed in the same room but in separate cages. In this study it appeared that close proximity with social companions was a main factor in the vocal plasticity exhibited by their subjects.

Social factors are well known as important in the acquisition of new vocalisations (Baptista & Petrinovich, 1984, 1986; Clayton, 1988; Slater *et. al.,* 1988; Pepperberg, 1990). Farabaugh *et. al.* (1994) investigated the importance of social factors in the learning of contact calls in adult budgerigars. They found that call type convergence between previously unfamiliar birds is achieved through mutual vocal imitation of social companions. In the absence of social but not aural contact, vocal imitation is greatly reduced.

The question that arises from the study by Farabaugh *et. al.* (1994) is whether social factors are really vital for vocal imitation, or whether a relevant but less salient stimulus is sufficient for copying to occur in the budgerigar. Some species of birds prefer conspecific learning [e.g. white-crowned sparrows, *Zonotrichia leucophrys* (Baptista & Morton, 1981; Baptista & Petrinovich, 1984, 1986); and song sparrows, *Melospiza melodia* (Marler & Peters, 1977, 1987; Baptista, 1988)], but they may require vocal or visual interaction with a live tutor for complete allospecific learning to occur. Young swamp sparrows can be trained with tape recordings (Marler & Peters, 1982) and Marler (1970) found that young male white-crowned sparrows could copy songs from taped conspecific playbacks if they were presented during the sensitive phase of 10 to 50 days, although Baptista & Petrinovich (1986) succeeded in showing that this species can learn thereafter by using live adult male tutors.

The potential of the psittacines for imitation, even of non-conspecific sounds, is well documented (Pepperberg, 1988, 1990). Much of the work on vocal learning in mimetic species has been carried out in the field of psychology, with the aim of teaching the subjects human speech; hand-reared parrots and corvids will accept humans as conspecific substitute social companions (Lorenz, 1970b; West *et al.*, 1983).

Several studies have attempted to teach various mimetic species from tapes in social isolation. There was either little or no learning, by Indian hill mynahs (*Gracula religiosa*, Grosslight *et al.,* 1964; Grosslight and Zaynor, 1967). Similarly budgerigars, black-billed magpies (*Pica pica*), a yellow-headed parrot (*Amazona ochrocephala*), and a grey parrot (*Psittacus erithacus*) could not learn from tapes in isolation (Mowrer, 1952, 1954, 1958). The tutoring of a grey parrot by an interactive human model however, resulted in the acquisition of speech patterns and a substantial vocabulary (Todt, 1975; Pepperberg, 1981, 1990). Social interaction with a tutor was obviously very significant in the success of these experiments, though learning from tapes might

have occurred had the models been exposed to conspecific vocalisations instead of human speech.

This chapter aims to investigate whether a mimetic species, the budgerigar, can learn new conspecific vocalisations from tapes in social isolation. The budgerigar is an age-independent species that can acquire new vocalisations throughout adulthood by mutual imitation of social companions, and social factors have been shown to greatly facilitate this process (Farabaugh, 1994). However, whether or not social factors are vital in the learning of new conspecific contact calls has not, as yet, been tested.

4.2. Methods

A total of 10 adult male budgerigars (*Melopsittacus undulatus*) that were at least one year old, and which had been housed together for three months prior to the commencement of the experiment in an outdoor aviary, were recorded in a sound attenuation chamber fitted with a Seinnheiser MD 400 microphone (frequency response of 1000-10 000 Hz, $\pm$ 6dB) and a Sony SRS-A20 speaker for playbacks. A sample of 50 calls were obtained from each bird and the dominant call classified by eye using the DSP Kay Digital Sonagraph model 5500. The dominant call was defined as that which was uttered by a bird on the majority of occasions, and in most cases represented over 80% of an individual's vocal repertoire during isolation. Figure 4.1. shows a selection of contact call types given by one individual. Each bird can have a call repertoire of between five and twenty call types. All birds in this experiment shared the same dominant call before the experiment (see Figure 4.2.).

Birds were then individually isolated for an eight week period in soundproof boxes within a cage 50 x 50 x 40cm (see Figure 4.3.). They were kept in the boxes for two days before commencement of the experiment to allow the them to settle in their new

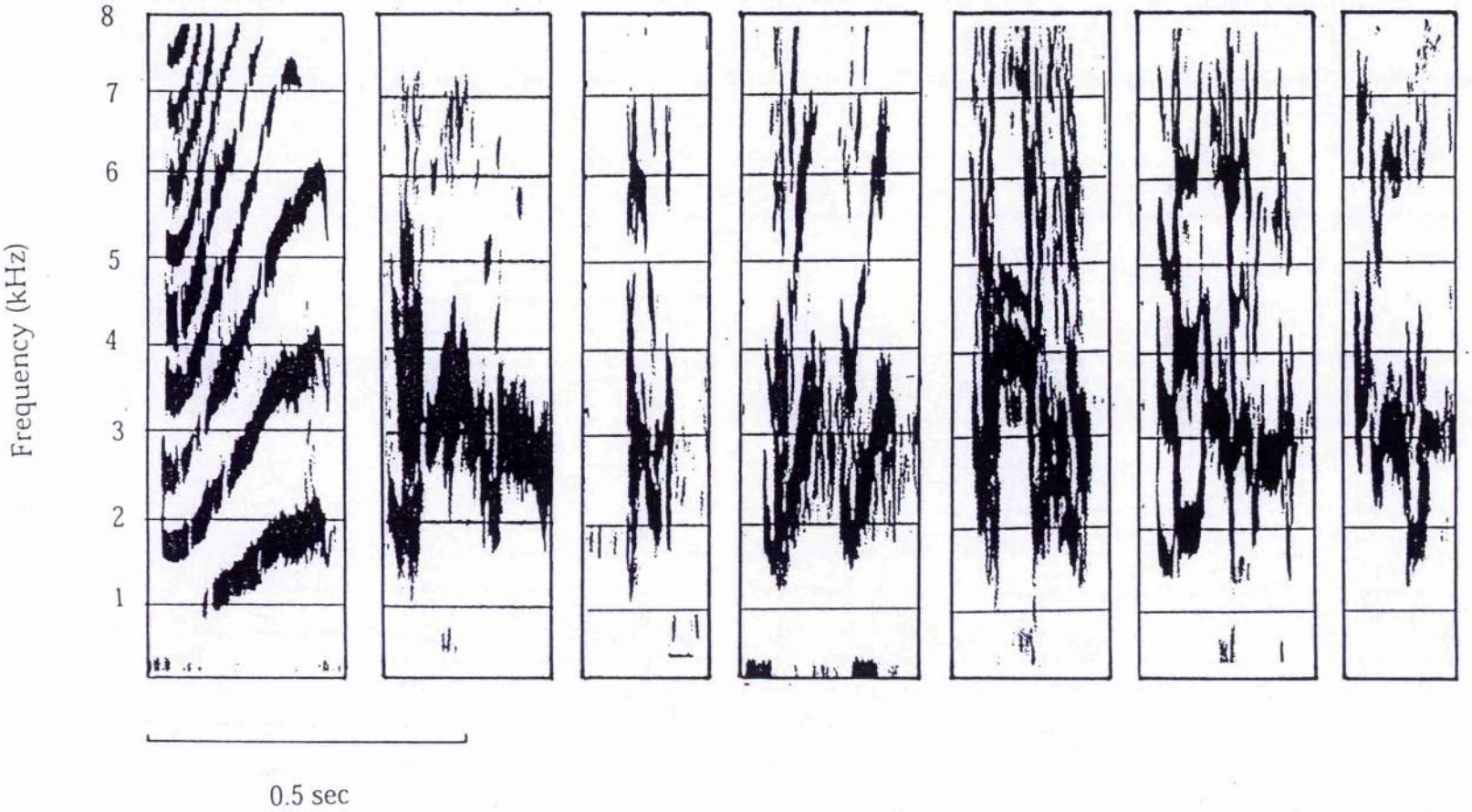


Figure4.1 range of contact call types given by a captive budgerigar. The dominant contact call is that given by a bird on approximately 80 % of occasions.

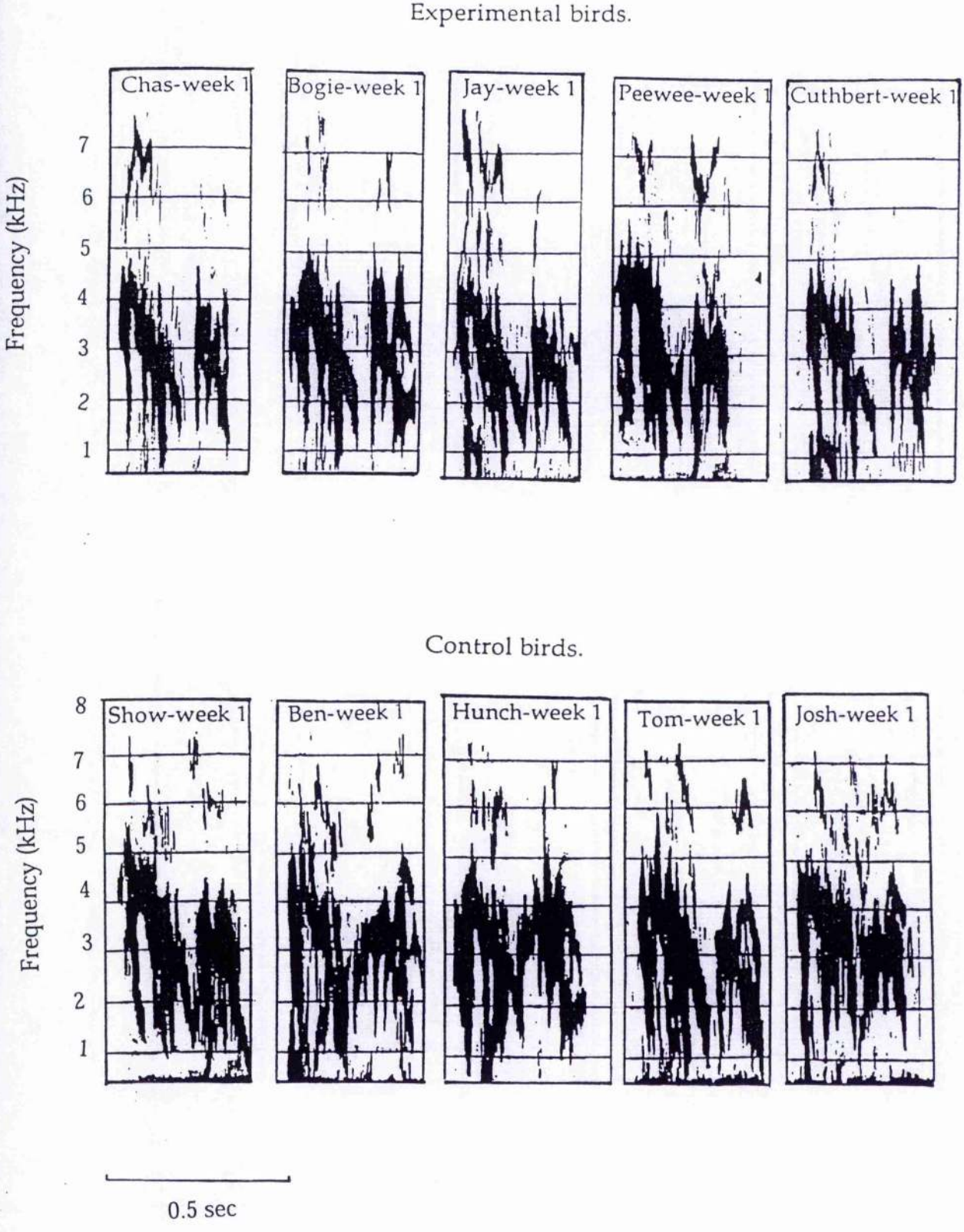


Figure 4.2. The group specific dominant contact calls shared by all ten experimental subjects prior to the commencement of the experiment.

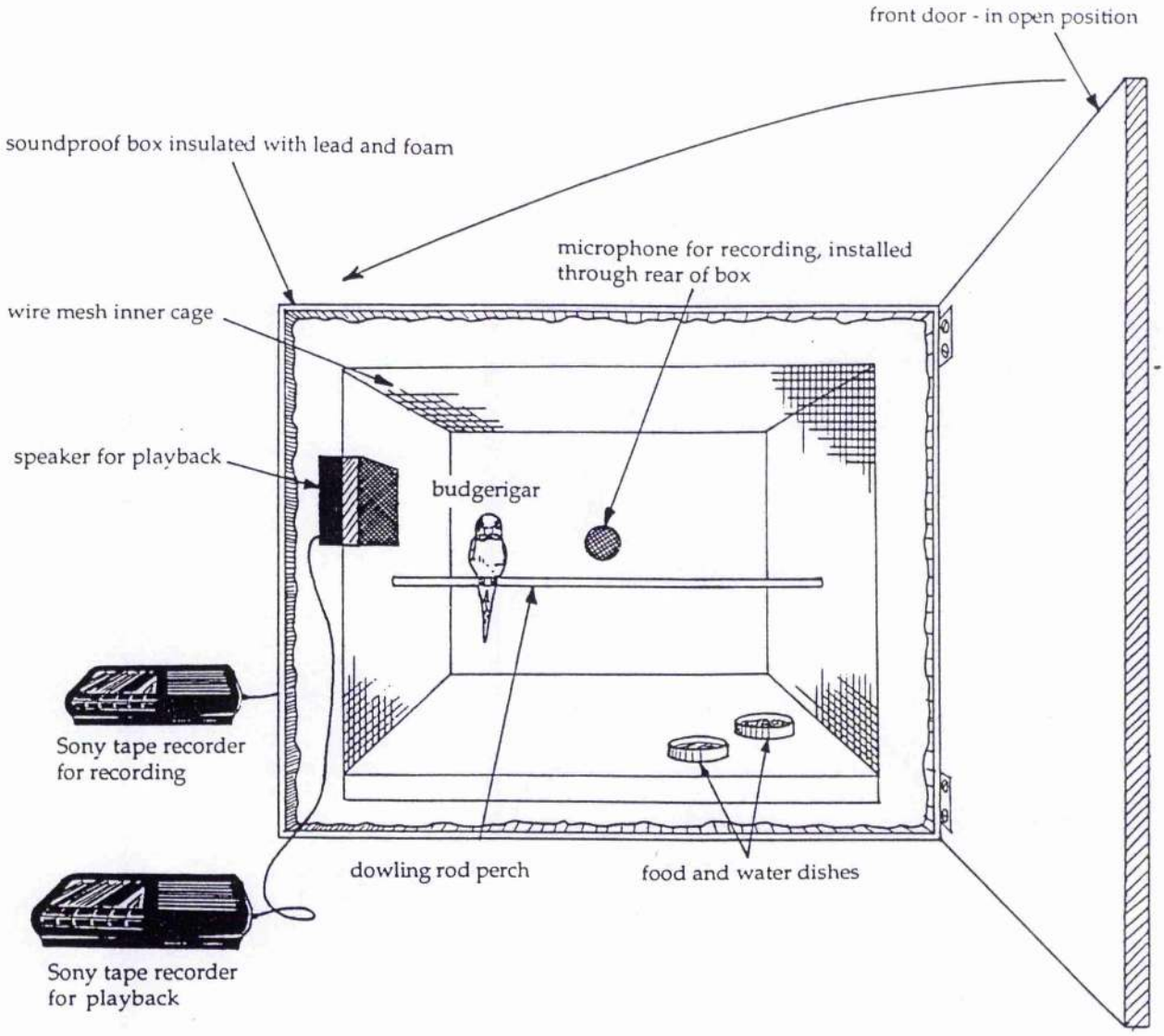


Figure4.3.Soundproof box in which each budgerigar was housed for the 8 weeks of the study.

environment. During the eight weeks the birds received a daily 14/10 light/dark cycle and were fed on budgie 50/50 mixture and watered daily, which involved opening the cage for a period of one minute or so. The temperature was maintained at between 20-25°C, with a relative humidity of 40-70%. Birds were also removed every four days for about 20 minutes and moved to another room where their calls were recorded within a sound attenuation chamber.

The budgerigars were split into two groups consisting of five birds in each. One group was the experimental group and each bird received, in isolation, a playback recording 'model' of a stranger conspecific for 15 minutes every hour during the 14 hours of simulated daylight within its soundproof box. This constituted a total of 210 minutes of playback every day. The playback recording had been made from one unfamiliar bird with which none of the subjects would have had previous experience. This inidividual had been recorded within a sound attenuation chamber and then copied onto two minute looped tapes for the playbacks.

Tapes were played through Marantz cassette recorders mounted inside the boxes. The quality of the playback was tested by recording from the looped tape whilst it was playing in the sound attenuation chamber, and analysing the recording on the DSP sonagraph. The second group was the control and received a looped recording of white noise for 15 minutes every hour instead of the conspecific playback. This was to account for any effects of the tape recorder functioning other than the conspecific playbacks that the experimental group received.

All birds were recorded every four days to trace the development of their dominant calls over time. Budgerigars were removed individually from the soundproof boxes and recorded in another room within a sound attenuation chamber. They were not removed from their boxes for more than 20 minutes, during which time a sample of about 50 calls was collected. The budgerigars could neither hear, see, nor interact in any way

with other conspecifics other than the playbacks during the whole 10 weeks of the study. After eight weeks all budgerigars were removed from isolation and individually recorded for a last time before being rehoused in an outside aviary. Whilst in the aviary, the budgerigars were recorded briefly with a directional microphone and the recordings analysed on the DSP sonagraph in order to ensure that the call types uttered in isolation were indeed the same as the dominant contact calls that were used within a social context.

Calls were firstly analysed by eye using the Kay DSP digital Sonagraph to detect whether there were any obvious changes in the structure of the calls. These assessments by eye were also used as a backup verification of the results of the cross-correlation, so that if any peak correlation values were in excess of that which was expected from observation, the methodology could be rechecked for any errors.

The same recordings were then analysed by the SIGNAL software (Engineering Design version 3.0) using cross-correlation of the digitised sonagrams along the time axis (using a Hanning window; sampling rate of 20 000 kHz; upper frequency limit of 8 kHz; Fast Fourier Transfer (FFT) size of 512; FFT interval of 13.2 sec; frequency resolution of 39.1 Hz; time resolution of 25.6 msec). Cross-correlations were performed between experimental birds' calls at every four day interval versus the 'model' call and control birds versus the 'model' call. This was to examine whether the experimental birds' calls had converged any more to the conspecific playback compared to the control group. The control birds were not exposed to any conspecific vocalisations over the test period and their calls were therefore expected to remain relatively unchanged.

Comparisons were also made within individuals over time in both control and playback groups to assess whether any change had occurred in their calls over time. This was to determine whether spontaneous change still occurred in the contact calls of budgerigars

(Farabaugh (1994) refers to the synchronous change of the group specific call over time) when isolated from interacting conspecifics.

4.3. Results

Analysis was firstly carried out on an individual basis to see whether there were any significant changes in the dominant contact call over the duration of the study. Cross-correlations were performed between the calls of each individual at each four day interval, and the original recordings of the calls that were made prior to the commencement of the study. Five examples of each bird's dominant contact call were compared with five examples of the original baseline call.

Figure 4.4.1.-4.4.5. shows the results of intra-individual comparisons for the experimental birds that received the playback model. The PCVs at the start of the experiment for the budgerigars, ranged from 0.95 to 0.85. Three of the birds did not deviate greatly from this mean, but two birds did. In Fig.4.4.1. and Fig.4.4.3. for Peewee and Cuthbert respectively, there is a marked decrease in the PCV with time, indicating that the similarity between the original call and subsequent recordings of the call was becoming less. The decrease does however, appear to level off on about the 40th day of the study, at approximately 0.75 for Peewee and 0.80 for Cuthbert, indicating a stabilisation of the new call variant. For the birds named Chas, Bogie and Jay, there is little or no suggestion of any change in their contact calls' structure with time.

The data for the first seven recording sessions (until day 25) were compared statistically with those from the last seven recording sessions (from day 29 to day 53) to detect whether there was any significant increase in the PCV over the duration of the study. A bootstrapping analysis was employed in which 500 random comparisons of the data set

Fig.4.4.1. Peewee

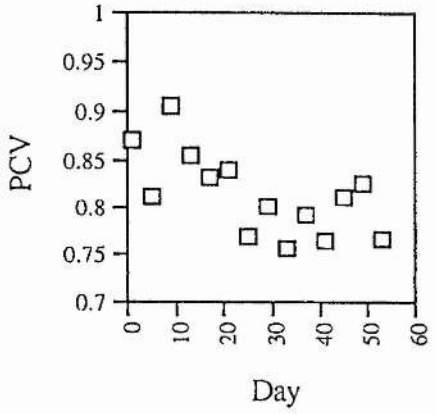


Fig.4.4.2. Chas

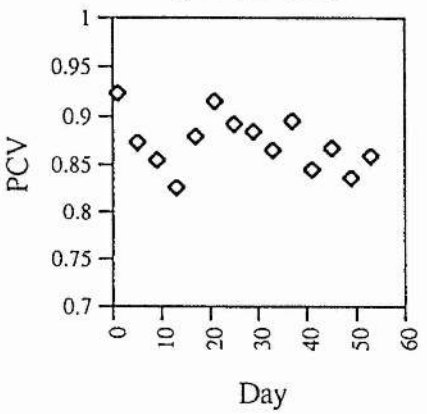


Fig.4.4.3.Cuthbert

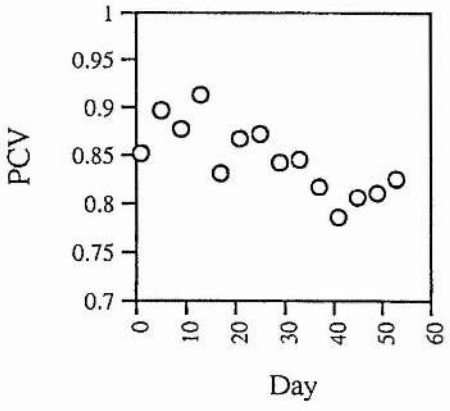


Fig.4.4.4. Bogie

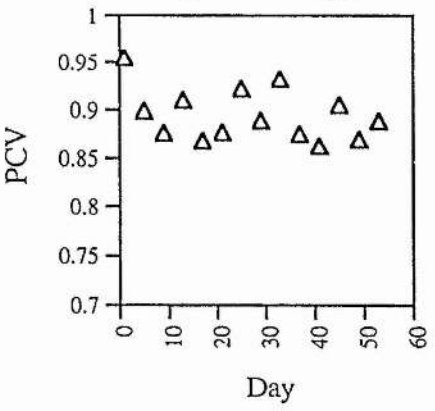


Fig.4.4.5. Jay

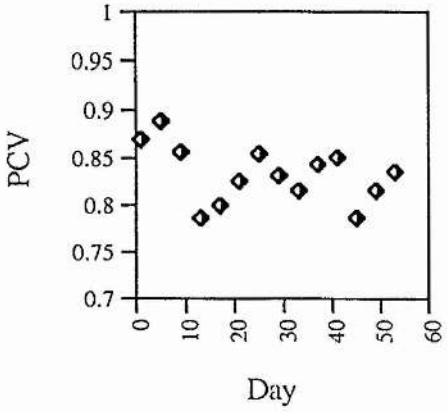


Fig.4.4.1.-4.4.5. Intra-individual changes in dominant contact calls with time in experimental budgerigars that the received playback. The peak correlation values (PCV) are derived from cross-correlations between the original recordings of each bird and the subsequent recordings at each recording session.

were made. The z-scores derived from the bootstrapping population and the experimental data set are shown in Table 4.1.

The results of the bootstrapping analyses appear to reflect the trends suggested by Fig. 4.4.1-4.4.5. There was a significant change in the PCV between the first stage of the study and the last stage for Peewee and Cuthbert. For Cuthbert the z-score indicates significance at the $P<0.01$ level, and for Peewee at the $P<0.05$ level, as can be seen in Table 4.1. For Chas, Bogie and Jay, there was no significant change in the dominant contact call over time, and therefore no apparent convergence with the model playback occurred.

Figures 4.5.1.-4.5.5. show the intra-individual change over time for the control birds. There is no apparent change in the dominant contact call for any of the individuals in the control group, and this is confirmed by the results of the bootstrapping analyses. Table 4.2. shows the z-scores for the control group. None of the values are above the threshold value of 1.96 for the difference to be significant at $P=0.05$. These birds' contact calls were therefore fairly stable during the eight weeks.

To assess whether any of the budgerigars in the experimental group had converged in the structure of their calls to the tape playback during the 10 weeks of the study, five samples of the dominant contact call from each individual at each four day interval were compared by cross-correlations to the 'model' playback.

Figures 4.6.1.- 4.6.5. show the results of cross-correlations between the five experimental subjects and the unfamiliar model playback. The peak correlation values (PCV) in all five figures are initially between 0.65 and 0.7, the similarity between birds being attributable to the fact that they all shared the same dominant contact call type and were therefore equally similar to the model call.

Individual	comparison	z-score	Probability of significance
Peewee	weeks 1-7 & weeks 8-14	2.03	P<0.05 significant
Chas	weeks 1-7 & weeks 8-14	0.908	P>0.05 not significant
Cuthbert	weeks 1-7 & weeks 8-14	2.78	P<0.01 significant
Bogie	weeks 1-7 & weeks 8-14	0.747	P>0.05 not significant
Jay	weeks 1-7 & weeks 8-14	1.39	P>0.05 not significant

Table 4.1. Z-scores derived from bootstrap analysis of the differences in the peak correlation values (PCV) between the beginning and end of the study for budgerigars that received the playback. The PCVs were derived from cross-correlations between each individual's call at every 4 day interval, and the original recording of the bird before commencement of the study. It therefore represents the degree of change of the subjects calls over the duration of the study. A z-score of 1.96 (P=0.05) or above, or in excess of 2.58 (P=0.01) represents a significant differences between the time periods and indicates that the call has changed.

Individual	comparison	z-score	Probability of significance
Show	weeks 1-7 & weeks 8-14	1.51	P>0.05 not significant
Ben	weeks 1-7 & weeks 8-14	0.752	P>0.05 not significant
Josh	weeks 1-7 & weeks 8-14	0.409	P>0.05 not significant
Tom	weeks 1-7 & weeks 8-14	0.166	P>0.05 not significant
Hunch	weeks 1-7 & weeks 8-14	0.675	P>0.05 not significant

Table 4.2. Z-scores derived from bootstrap analysis as in Table 4.1. but for control budgerigars that were not exposed to a playback. All z-scores are below 1.96 (P=0.05) indicating no significant change in the call for all control birds.

Fig.4.5.1. Show

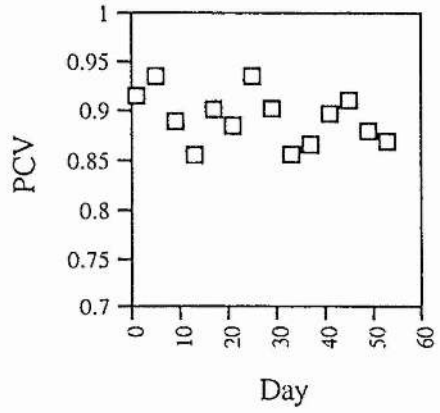


Fig.4.5.2. Ben

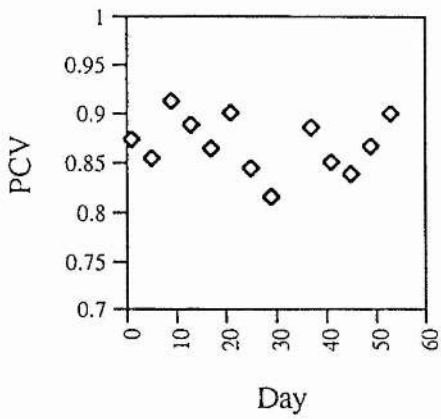


Fig.4.5.3. Josh

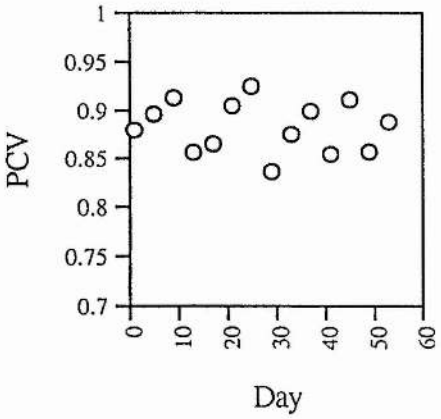


Fig.4.5.4. Tom

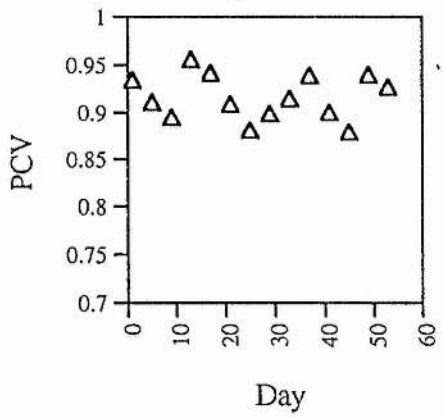


Fig.4.5.5. Hunch

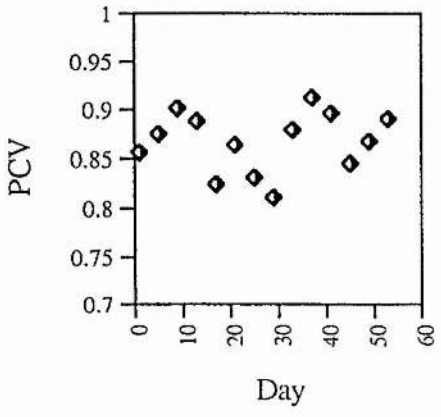


Fig.4.5.1.-4.5.5. Intra-individual changes in dominant contact calls with time in control budgerigars that the received playback. The peak correlation values (PCV) are derived from cross-correlations between the original recordings of each bird and the subsequent recordings at each recording session.

Fig.4.6.1. Peewee with model

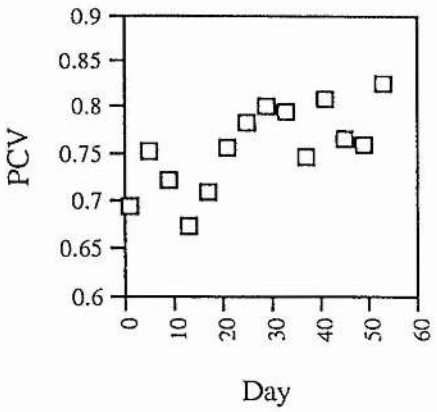


Fig.4.6.2. Chas with model

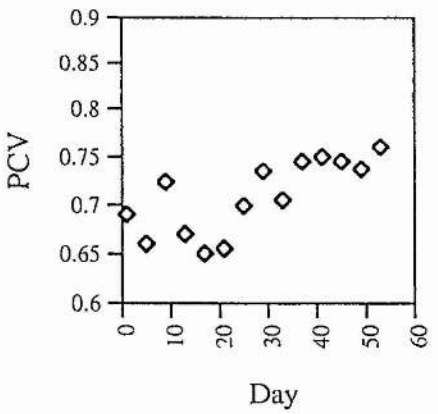


Fig.4.6.3. Cuthbert with model

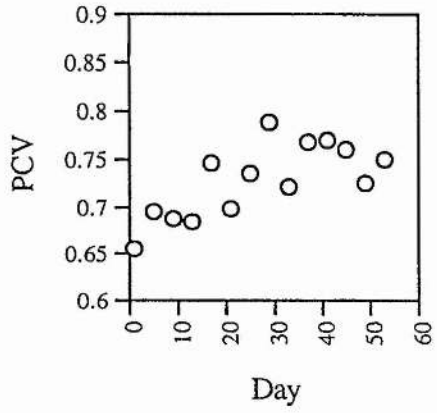


Fig.4.6.4. Bogie with model

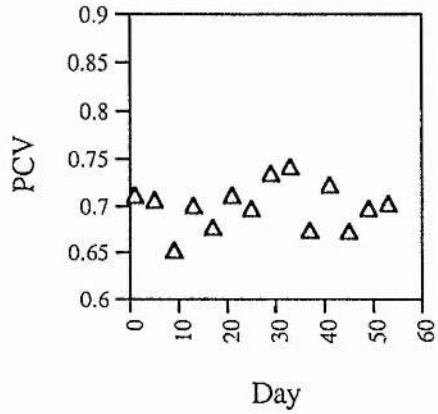


Fig.4.6.5. Jay with model

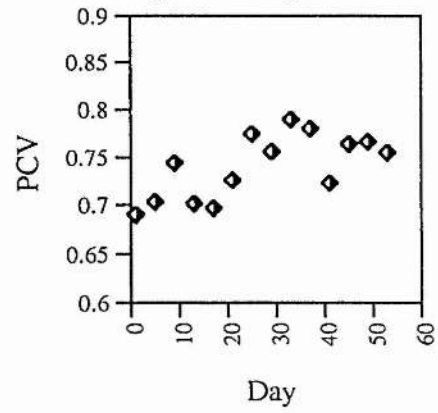


Fig.4.6.1.-4.6.5. Changes in the similarity between the dominant contact calls and the playback model with time in experimental budgerigars that the received playback. The peak correlation values (PCV) are derived from cross-correlations between the recordings of calls at each 4 day interval and the playback model.

Most birds, with the exception of the individual 'Bogie' (Fig. 4.6.4.), showed a tendency for a slight increase in the PCV with time. In Peewee (Fig.4.6.1.) and Cuthbert (Fig.4.6.3.), this increase was more marked, with an increase from 0.7 to 0.8, and 0.65 to approximately 0.75 respectively. The increase in PCV in Chas and Jay was about half that in the other two birds.

A bootstrap analysis was carried out on the individual-model data, as for the previous intra-individual data. There was a highly statistically significant difference in the PCVs between the first and second part of the study in two of the birds; Peewee and Cuthbert ($P<0.01$), as seen in Table 4.3. Jay, and to a lesser extent Chas, had z-scores which approached significance at $P<0.05$ level. In contrast, Bogie did not exhibit any significant change in its PCV over the eight weeks of the study.

The PCV for a cross-correlation between two recordings of the same contact call type from each bird prior to commencement of the study was between 0.85 and 0.95; this represented a standard PCV for essentially identical call types (not the same recording duplicated). For the two birds that appeared to show evidence of copying the model, Peewee and Cuthbert, the PCV resulting from cross-correlations between their respective contact calls at the end of the study and the model playback, was 0.85 for Peewee and 0.75 for Cuthbert. This suggests that reasonably accurate copies of the model may have been produced, at least in Peewee, although the PCVs were not as high as those between comparisons of the same call.

Fig. 4.7 illustrates the process by which it was determined whether birds had accurately copied the model playback. The call of each bird at the end of the study was compared with the model playback to obtain PCVs that were expectantly lower than the comparisons of similar calls before the experiment. These values were then compared by bootstrapping with the PCVs of similar calls (standard PCVs representing essentially

Individual	comparison	z-score	Probability of significance
Peewee	weeks 1-7 & weeks 8-14	2.47	P<0.01 significant
Chas	weeks 1-7 & weeks 8-14	1.4	P>0.05 not significant
Cuthbert	weeks 1-7 & weeks 8-14	2.55	P<0.01 significant
Bogie	weeks 1-7 & weeks 8-14	0.19	P>0.05 not significant
Jay	weeks 1-7 & weeks 8-14	1.88	P>0.05 not significant

Table 4.3. Z-score results derived from bootstrap analysis of the differences in the peak correlation values (PCV) between the beginning and end of the study for budgerigars that received the playback. The PCVs were derived from cross-correlations between each individual's calls at every 4 day interval, and the model playback, and therefore represents the degree of similarity between the subjects calls and the model over the duration of the study. A z-score of 1.96 (P=0.05) or above, or in excess of 2.58 (P=0.01) represents a significant difference between the time periods and indicates that the call has changed.

Individual	comparison	z-score	Probability of significance
Show	weeks 1-7 & weeks 8-14	0.346	P>0.05 not significant
Ben	weeks 1-7 & weeks 8-14	0.655	P>0.05 not significant
Josh	weeks 1-7 & weeks 8-14	0.389	P>0.05 not significant
Tom	weeks 1-7 & weeks 8-14	0.117	P>0.05 not significant
Hunch	weeks 1-7 & weeks 8-14	0.870	P>0.05 not significant

Table 4.4. Z-scores derived from bootstrap analysis as in Table 4.3. but for control budgerigars that were not exposed to a playback. All z-scores are below 1.96 (P=0.05) indicating no significant change in the call for all control birds.

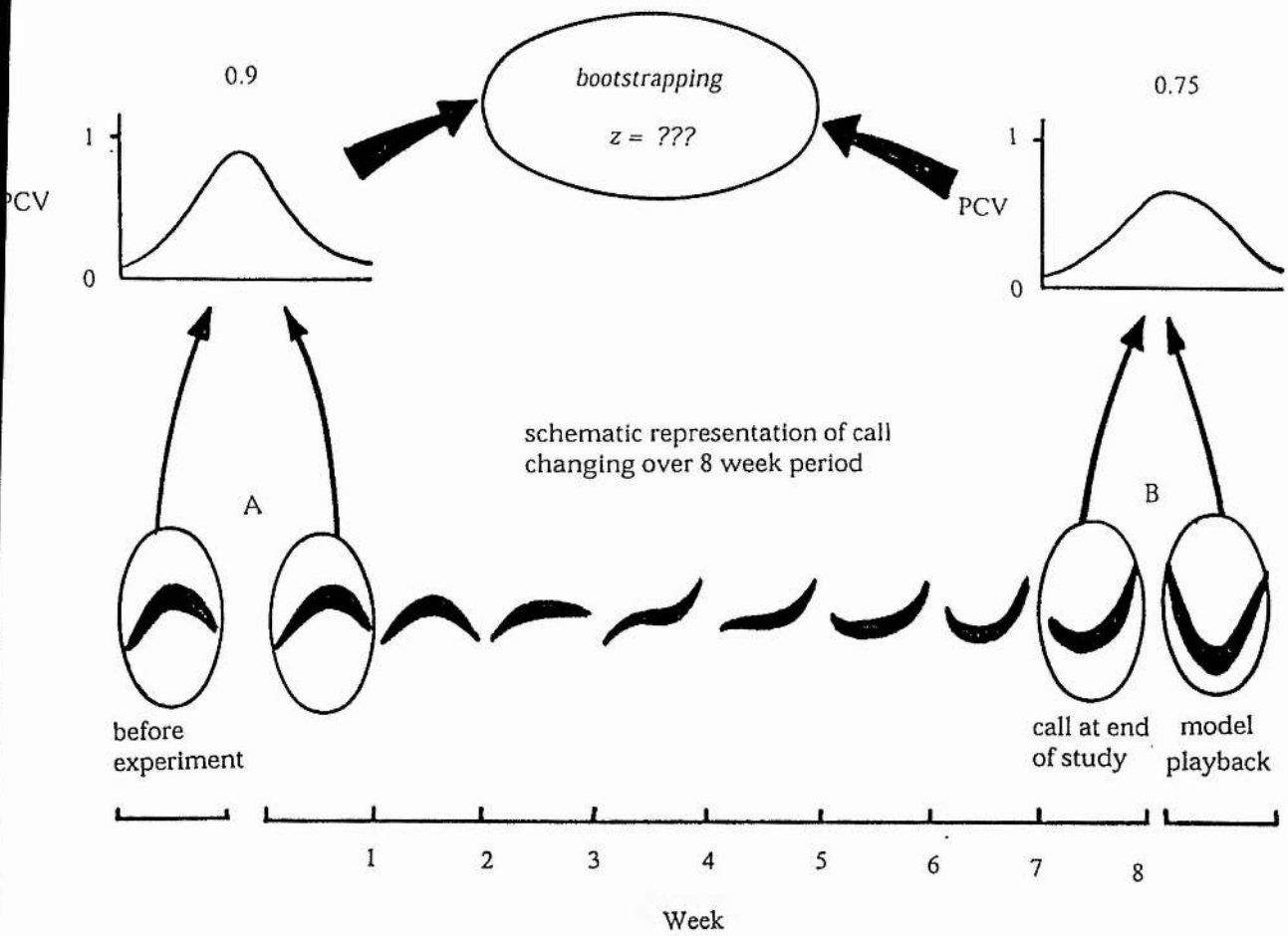


Fig. 4.7 Method of assessing whether birds had produced accurate copies of model playback

A The initial recording (before the birds were isolated for the 8 week duration of the study) was compared with a similar recording of the call made just prior to the experiment. These were essentially identical calls and revealed correspondingly high peak correlation values (PCVs) e.g. 0.9. A value of 0.9 ± a range, could be considered as representing calls that were essentially the same, and provided a standard against which comparisons of the call at the end of the study and the model playback could be assessed.

B The call at the end of the 8 weeks was then compared with the model sample to which the birds were exposed to during 8 weeks. The corresponding PCVs were expected to be lower because the calls were not from the same individual. The extent of call matching between the experimental birds' calls and the taped call would be revealed by the PCV score. Judging whether a PCV of e.g. 0.75, indicates a good copy is subjective. Therefore, as a standard of expected PCVs between identical calls, the values obtained in A were used, against which PCVs from the end calls with the model were compared by bootstrapping. If the PCVs of 'call at the end versus model call' were significantly lower than those of 'call of same bird before the study', then we can conclude that the bird has not copied the model.

identical calls; see above for explanation) to determine whether birds had produced near identical copies of the playback by the end of the eight week period.

The z-scores for these two comparisons were 1.96 (P=0.05) and 2.61 (P<0.01) for Peewee and Cuthbert respectively. Cuthbert's call was significantly different from the model playback and did not therefore produce an accurate copy of the model playback; the z-score for Peewee falls exactly on the threshold value for showing a difference between the two tested samples.

In comparison to Figures 4.6.1. - 4.6.5. for experimental birds, Figures 4.8.1.-4.8.5. show that the PCVs of all control birds appeared to show no obvious trend to increase or decrease with time, despite fluctuations in the PCV with each recording session of about 0.1. Though these birds did not receive a conspecific playback stimulus, and were therefore not expected to have converged on the model call, it was necessary to see whether birds not exposed as such, would still undergo spontaneous change in their calls that, by mere coincidence, became more similar to the model call. This was not the case, with all control birds having fairly stable contact calls.

Table 4.4. shows the z-scores resulting from bootstrapping analysis of the control group's data. As in the experimental group, PCVs for the first 7 recording session of the study were compared with those of the last 7 recording sessions. All z-scores resulting from the bootstrapping are far below the threshold value of 1.96 (P=0.05) for significance. Their calls clearly remained fairly stable in structure throughout the study.

Sonagrams of the dominant contact calls of all 10 individuals at the start and end of the eight week study are shown in Figures 4.9.1. and 4.9.2. for experimental and control groups respectively. In Fig. 4.9.1., sonagrams of the dominant contact calls of Cuthbert and Peewee, the individuals which showed most convergence to the playback model, are shown at the intermitent intervals of week three and five in order to illustrate the

Fig.4.7.1. Show with mode

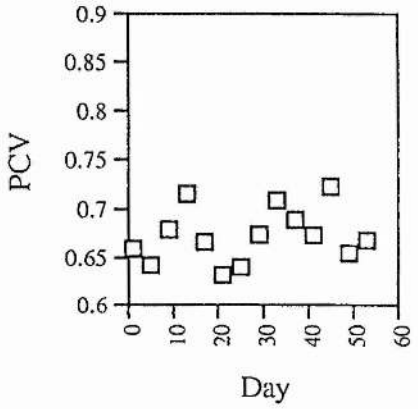


Fig.4.7.2. Ben with model

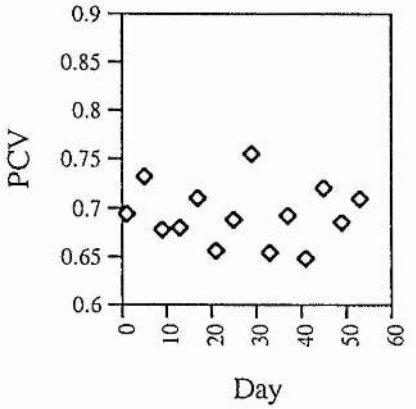


Fig.4.7.3.Josh with model

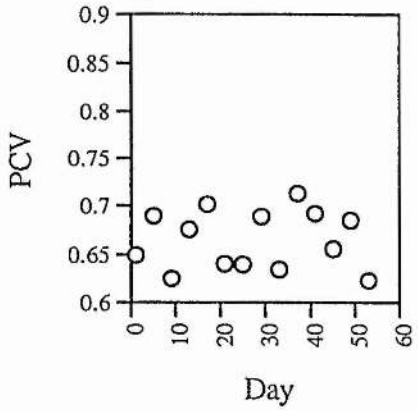


Fig.4.7.4.Tom with model

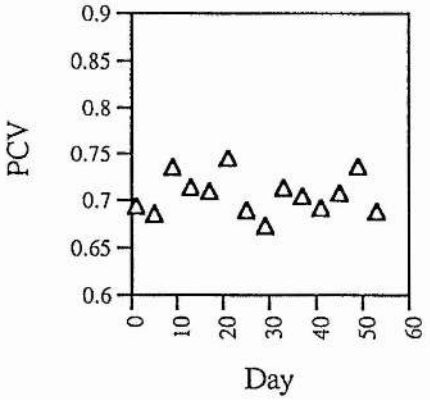


Fig.4.7.5.Hunch with model

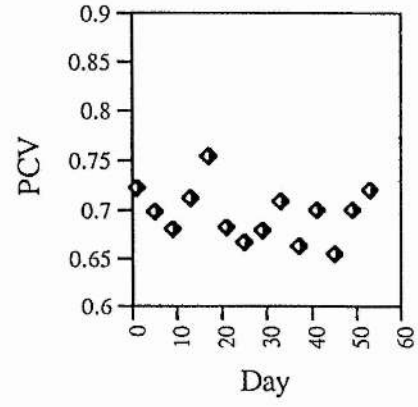


Fig. 4.8.1-4.8.5 Changes in the similarity between the dominant contact calls and the playback model with time in control budgerigars that did not receive the playback. The peak correlation values (PCV) are derived from cross-correlations between the recordings of calls at each 4 day interval and the playback model.

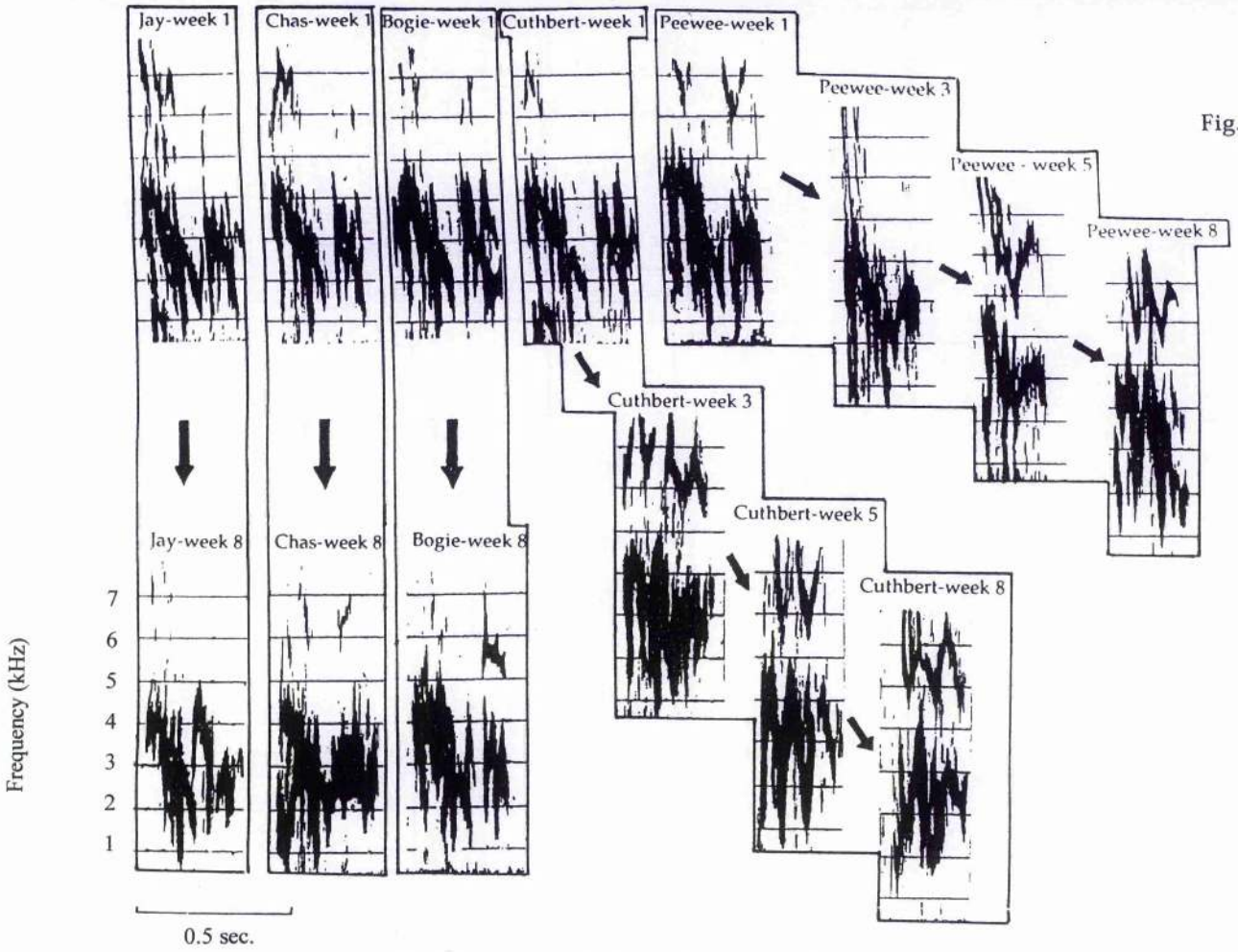


Fig. 4.9.1 E

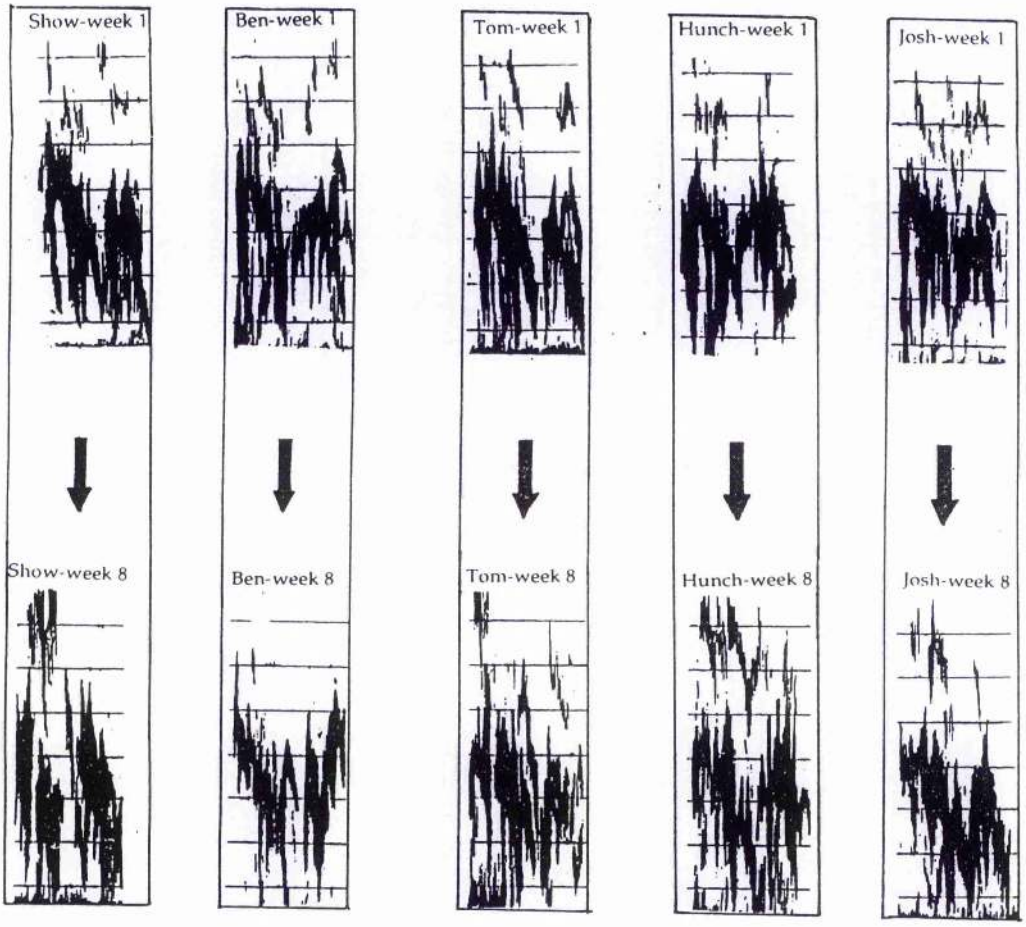


Fig. 4.9.2 C

gradual change in the frequency modulations. Although it can be seen from these sonagrams that the copying of the playback was by no means exact, some of the main characteristic modulations are present in the calls of these two birds, hence their higher PCVs with the model call.

The sonagrams of the calls of the three remaining experimental birds (fig. 4.9.1.), and those of the five control birds (fig. 4.9.2.) do not resemble as closely the sonagrams of the calls in week one, and this is probably the result of spontaneous mutations in the structure of the call after eight weeks of isolation.

4.4. Discussion

The potential of the Psittacines for vocal imitation is well known (Pepperberg, 1988, 1990). Indeed, in a few exceptional cases, parrots have been taught to respond to instructions from human tutors with the appropriate English vocabulary, and to combine several words to form distinct speech patterns (Todt, 1975; Pepperberg, 1981). In these cases though, social interaction with a live tutor was considered a prerequisite for the success of learning in the subjects.

The relative contribution that social influences have on the learning process appears to differ between species of birds. For instance, it has been shown that young swamp sparrows will learn accurately from playbacks of conspecific songs with a complete lack of any social stimulus (Marler & Peters, 1982), but this is only possible when the bird is predisposed to be at its most attentive, during the sensitive phase.

In contrast the importance of social factors in the song learning of zebra finches has long been stressed (Immelman, 1969). Eales (1989) found that young male zebra finches do not passively copy songs that were played through loudspeakers. Adret

(1993) was able to demonstrate that young birds would learn from tapes, but only if they were housed in a Skinner box and were required to peck a key for a song 'reward'. In this case, the interaction between the bird pecking a key and the Skinner box 'responding' with conspecific song appeared to provide an adequately salient substitute for the lack of social stimuli from other zebra finches.

Brown, Dooling and O'Grady (1988) reported that adult budgerigars housed together in one cage, shared a contact call type that differed from the contact calls of other birds in different cages in the same room. In this experiment it is likely that there was no copying between different groups in separate cages, because of the presence of appropriate live conspecific models within an individual's immediate environment.

Farabaugh *et. al.'s* study (1994) reflected the findings of Brown, Dooling and O'Grady, in that unfamiliar budgerigars that were housed together in shared cages converged in their dominant contact calls. They did, however, find evidence that limited copying between groups in separate cages also occurred; two of the eight shared contact call types were shared by birds in different groups. Therefore, although call convergence through mutual vocal imitation was more pronounced among budgerigars that could see, hear, and interact with one another in the same cage, there was a slight amount of copying with aural but not social contact.

The results of this chapter suggest, based on the significant changes in the dominant contact calls of two individuals, that some budgerigars can, when placed in social isolation, learn a limited amount from taped recordings of conspecifics. One bird in particular, produced a call type by the end of the eight weeks that was very similar to the call of the taped playback it had heard over this period. Though this call was not a completely accurate copy, it had nevertheless, significantly converged on the model, and shows clear evidence of the ability to learn with only aural stimulation, and with a complete lack of any social context.

Brown, Dooling and O'Grady (1988) found no imitation of budgerigars in separate cages, even though they could see and interact with each other at a distance. Such an experimental set up enables the subjects to actively interact with one another between cages, calling and responding to specific individuals or to the group as a whole. It is therefore perhaps suprising that there was not even a limited amount of cross-group imitation, as Farabaugh *et al.* (1994) found between their captive groups of budgerigars, in which accurate copying of contact calls was achieved.

The importance of interactive learning, in which vocal interaction with a conspecific stimulus has reinforcing properties, has been demonstrated in juvenile chaffinches, *Fringilla coelebs* (Stevenson, 1967, 1969) and zebra finches (ten Cate, 1991). In the present study, there was no interactive component; birds were simply exposed to the same two minute playback loop for 15 minutes every hour for 14 hours a day. Therefore, if birds responded to the playback there would not have been the hightened motivation and escalating calling frequency between two duetting birds, which is usually observed within an interacting conspecific group.

Nevertheless, the convergence that Peewee and Cuthbert exhibited was exceptional, and none of the remaining experimental birds even approached such changes in their dominant contact calls. In this respect, the ability to learn vocalisations appears to vary greatly between individuals and is also probably very dependent on the motivational state of the subjects. It may be, for instance, that the extreme social deprivation that the birds experienced for eight weeks, was too stressful for the majority to be settled enough to learn any new vocalisations. A detailed record of the behaviour of each budgerigar was not made, and therefore any possible effect of stress on the process of learning can only be speculative.

It is unlikely that the quality of the playback was responsible for the lack of learning in most birds in this experiment, since the playback itself was re-recorded and analysed on the DSP sonagraph to check the clarity of the sonagrams was not significantly different from that of the original playback recording. Adret (pers. comm.) had previously observed a lack of copying in young zebra finches that were exposed to playbacks through a video recorder, and later found that the quality of the output was not good, despite appearing to be adequate to the human ear. He repeated the experiment with more suitable recording equipment, with the result that the young birds were able to learn from the playbacks (Adret, 1993).

The control birds in the present study were necessary to confirm that any change in the experimental birds' dominant contact calls was due to the playback that they received, and not merely through spontaneous improvisation of the call. Farabaugh *et. al.* (1994) describe such changes in their experimental groups of budgerigars. Synchronous changes in the group specific call were said to evolve through partial imitation of cagemates, recombination, and improvisation. No such changes were apparent in the control group, which suggests that these changes do not occur spontaneously, but are instead triggered by the mutual effect of conspecifics reinforcing one another.

In the absence of any aural stimuli, a budgerigar's contact call remains fairly stable. This was unlikely to have been due to an inability to improvise new sounds or versions of calls, since 'improvisation' (i.e. the composition of new sounds), has been described in the process of new call acquisition (Farabaugh *et. al.,* 1994).

The functional significance of call convergence and synchronous changes in the group specific call in the species that exhibit it, is not known, so the reasons why individuals do not change their call in the absence of other conspecifics is equally speculative. It may be that calls change constantly in very subtle ways as a result of slight mistakes in copying and the reproduction of sounds, as has been suggested for the evolution of

dialects in some song birds (Slater & Ince, 1979; Williams & Slater, 1990). Individual 'mutations' in the call are likely to be small and not marked, but the cumulative effect of many small alterations by all members of a flock, which are then copied and accentuated by other individuals, may cause a significant shift in a call with the result of producing a new contact call type. This might be more likely to occur when new recruits, which are unfamiliar with the group specific call, join the flock.

Vocal imitation by adults may be adaptive in aiding recognition of and maintenance of contact with particular conspecifics and may also serve as a mechanism of integration of new members into a social pair or group (Brown, 1985; Feekes, 1977, 1982; Mundinger, 1970; Thorpe & North, 1965, 1966). In these respects, it may be important for individuals within a flock to constantly update their rendition of the group specific call, which changes constantly either through random copying errors or by specific alterations, so that each bird can maintain its identity within the social group.

Though the visual sense is likely to play a major role in individual recognition, vocal imitation may be so important as to result in antagonistic behaviour towards an individual that does not call like the group as a whole. Although in the wild there is frequent mixing of flocks without any apparent conflict (Brereton, 1963), in captivity, aggression by members of a flock towards an unfamiliar bird is occasionally observed when new individuals are added to an established aviary group . Within a matter of weeks, these new birds' dominant contact calls have usually converged on that of their flock mates (pers. observ.).

The social influences or pressure on individuals within a group to converge to the group specific call, must be high to result in the rapid call convergence that has been observed; Farabaugh *et al.* (1994) report evidence of call imitation between cagemates within one week of being housed together for the first time. In the absence of other conspecifics, there would appear to be no such motivation to change the call.

CHAPTER 5

THE IMPORTANCE OF SOCIAL FACTORS IN THE PROCESS OF CALL CONVERGENCE IN BUDGERIGARS

5.1. Introduction

Social factors are known to be important in the learning of song and other vocalisations (Baptista & Petrinovich, 1984, 1986; Slater *et al.*, 1988; Mann, 1991; Jones, 1994; Farabaugh *et al.*, 1994). Even in age-dependent species, social factors can extend the sensitive period (Kroodsma, 1982).

Much of the evidence for vocal mimicry comes from hand-reared animals which accept humans as conspecific social companions (Lorenz, 1970a; West *et al.*, 1983). This acceptance strongly implies a social factor in vocal learning which is so powerful that it overrides normal preferences for species-specific sounds. Therefore, it might be predicted that in normal social interactions with conspecifics, the group (pair, family, co-operative group or flock) is the central source of social influences on vocal learning. Learned vocalisations should reflect particular social relationships, resulting in shared sounds used in communication, both within and between groups.

The results in Chapter 4 demonstrated that the learning of new calls by adult male budgerigars was very limited when the model call was presented as a taped playback. This indicated the need for budgerigars to engage in some kind of social interaction with conspecifics: although we cannot conclude from the previous study that social factors are vital for learning to occur in adulthood, we can say that they play a very important role in the full acquisition of complete contact calls.

In Australian magpies (*Gymnorhina tibicen*), the social setting of imitation certainly involves members of the same social group; the higher percentage of syllable sharing by magpies in the same group, compared to magpies in different groups, reflects the vocal imitation of groupmates (Farabaugh *et al.*, 1988).

The influence that a salient interactive social stimulus can have on the process of vocalisation acquisition can be dramatic. Mundinger (1970, 1979) observed call convergence between two closely related species, pine siskins (*Carduelis pinus*) and European siskins (*C. spinus*), when they were housed together, and perhaps more remarkably Pepperberg (1981, 1990) found that a grey parrot could learn non-conspecific human language sounds and vocabulary if tutored by an interactive human model. Indeed, interactive-tutoring seems necessary for learning to occur in zebra finches (Adret, 1993).

Studies such as those of Pepperberg, illustrate rather strikingly how the addition of a social context can cause a bird to learn a sound that would not otherwise be acquired. Many studies have tended to concentrate rather too generally on the affects of the presence or absence of live tutors on the process of learning in bird species. Any enhanced ability to acquire new vocalisations by the addition of a live tutor was attributed to the necessity for social factors, without adequate consideration of exactly what it is about a live tutor that stimulates this increased receptivity to learn (Weary & Krebs, 1987).

Eales (1989) found that young zebra finches would copy from a tutor if they were permitted visual and vocal contact but no physical interaction. Learning was reduced if they were then deprived of visual contact by the addition of an opaque screen.

The proximity between tutor and tutee also appears to have a significant affect on the extent of learning. If zebra finches are tutored by a male that is housed a small distance

away in a separate cage, the amount of song that is learnt by the young bird is less than if they were both housed together (Adret, unpublished). Mann and Adret (unpublished) conducted a series of experiments in which they varied the distance between tutor and tutee by a wire lattice. Imposing a space in this manner, resulted in less copying by the young zebra finch.

Further studies by Adret (in prep.) showed the importance of physical interaction on learning. Visually isolating young birds from tutors by an opaque screen resulted in a lack of copying. However, if young birds were temporarily blinded with plastic eye-caps, but housed together with the tutor so that they could physically interact with one another, the subjects produced accurate copies of the tutor's song.

In budgerigars, social interaction appears to guide what is learned; young males preferentially imitate the abnormal syllables and temporal patterning of the warble song of their isolate-reared cagemates, rather than the normal warble song of birds in adjoining cages (Farabaugh *et al.*, 1992a).

Clayton (1987) carried out an experiment which investigated the affect of aggression on tutor choice in zebra finches. Young birds were housed with several potential adult male tutors and all behavioural interactions were observed. She found that the young zebra finches tended to learn their song from the tutor that was most aggressive to them, irrespective of the aggression or dominance rank between the two adult tutors. It would be tempting to conclude from these results that young birds were learning their song from a male which exhibited a conspicuous competitive advantage; a trait which may be be interpreted by other conspecifics in a population from a bird which shared this song. It may, however, be more likely that the higher aggression of the tutor was a consequence of the responsiveness of the young bird to it, although Jones and Slater (1996) argue otherwise.

Brown (1985) made observation of the ongoing processes involved in vocal sharing and concurrent social interactions of the American crow (*Corvus brachyrhynchos*). Syllable sharing varied according to social relationships; sibling dyads which allopreened significantly more, also shared the most song syllables. These findings suggest that learned, shared song is related to affiliative social bonds between particular individuals who know each other.

Several studies, which have already been discussed in previous chapters, have dealt with the process of call convergence in age-independent learners (black-capped chickadees (Mammen & Nowicki, 1981; Nowicki, 1989); American goldfinches (Mundinger, 1970, 1979); and budgerigars (Farabaugh *et. al.,* 1994). In these experiments, unfamiliar birds were housed together for several weeks and their calls converged to a common group specific one. Farabaugh *et al.* (1994), describe the process of call convergence as occurring through mutual imitation, in which all individuals copy one another to more or less the same extent, and are themselves copied. Initially though, they do describe imitation of one bird's original dominant contact call type by another bird, in which case, one bird's call served as the model that another bird imitated. A similar pattern of slow simultaneous change was found in the shared colony-specific songs of yellow-rumped caciques (*Cacinus cela*) (Trainer, 1989).

Brown *et al.* (1988) tested whether syllable sharing could result from vocal imitation of groupmates, using a three year old adult female Australian magpie which was hand-reared and accepted humans as conspecific substitutes. Within two weeks of exposure to a human, the magpie had incorporated an exact copy of a vocalisation into its repertoire and used it frequently. This demonstrated that vocal imitation results in shared sounds, and that at least some vocal imitation is related to group membership, and probably also affiliative social interactions.

This study aims to examine the process of call convergence in budgerigars more closely. Firstly, it will investigate whether imitation is mutual amongst all cagemates, or whether certain individuals tend to be copiers and others tutors. Secondly, it will attempt to relate the process of call convergence, whether mutual or otherwise, to behavioural data collected from each individual during the study. From this, it may be possible to determine exactly which social factors are important in determining the course and extent of call convergence.

5.2. Methods

5.2.1. Subjects and housing

The subjects were 12 adult male captively bred budgerigars (*Melopsittacus undulatus*), of various colour morphs. Each bird within an experimental group was obtained from a different breeder in order to ensure that none of the individuals had had any previous experience of one another. All subjects had been normally raised by the parents within an aviary colony breeding system, and exhibited normal social and vocal behaviours prior to their housing with the other experimental birds.

Each experimental group of budgerigars was kept in a cage 1.5m by 0.5m by 0.5m, with 6 dowling rod perches set across the cage horizontally (see Fig. 5.1). Budgerigars were fed with 50/50 budgie mixture from Haith's, and given fresh water daily. Each group was housed in isolation from other conspecific groups so that individuals could only interact with their other three cagemates for the 53 days of the study.

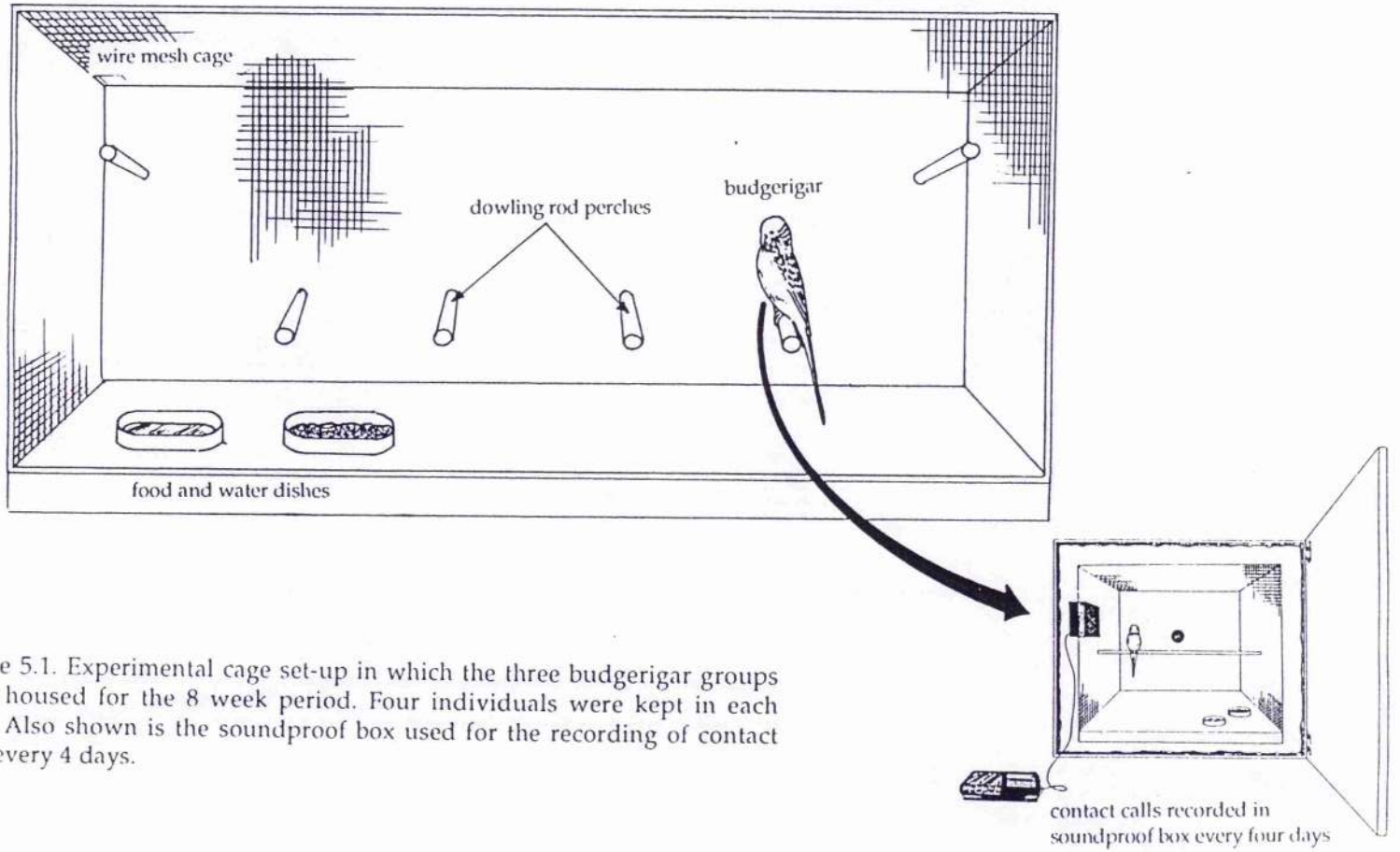


Figure 5.1. Experimental cage set-up in which the three budgerigar groups were housed for the 8 week period. Four individuals were kept in each cage. Also shown is the soundproof box used for the recording of contact calls every 4 days.

5.2.2 Sound Recording

Each budgerigar was recorded prior to the commencement of the experiment. Individuals were placed in a sound attenuation chamber (see Fig. 5.2), fitted with a Sennheiser MD 400 microphone (frequency response of 1000-10 000 Hz, ±6dB) and Sony SRS-A20 speaker for playbacks, and a sample of 100 calls was recorded. In some cases, if the bird did not vocalize, a recording of conspecifics in an aviary was played to it via the speaker. This playback was usually sufficient to stimulate the individual into responding vocally.

From this sample of calls each call type was classified by eye using the DSP Kay Digital Sonagraph model 5500, and the most common type selected (i.e. the call the birds uttered most frequently during the recording session). This call, which was always uttered on more than 80% of occasions, was termed the 'dominant contact call' of the individual and was that used to judge whether convergence had occurred (see Figure 4.1).

5.2.3 Experimental procedure

Birds were placed in the cages with three other strange budgerigars. None of the birds had either heard or seen their cagemates prior to this time. Each bird was recorded every four days in a sound attenuation chamber, with approximately 50 calls taken at each session, and in no case less than 10.

In addition to recording vocalisations, observations of social behaviours were made during two one hour periods every day. Observations were recorded at 30 second intervals, during which, several aspects of social behaviour were considered, providing an almost continuous recording schedule (allowing for the time to observe and record

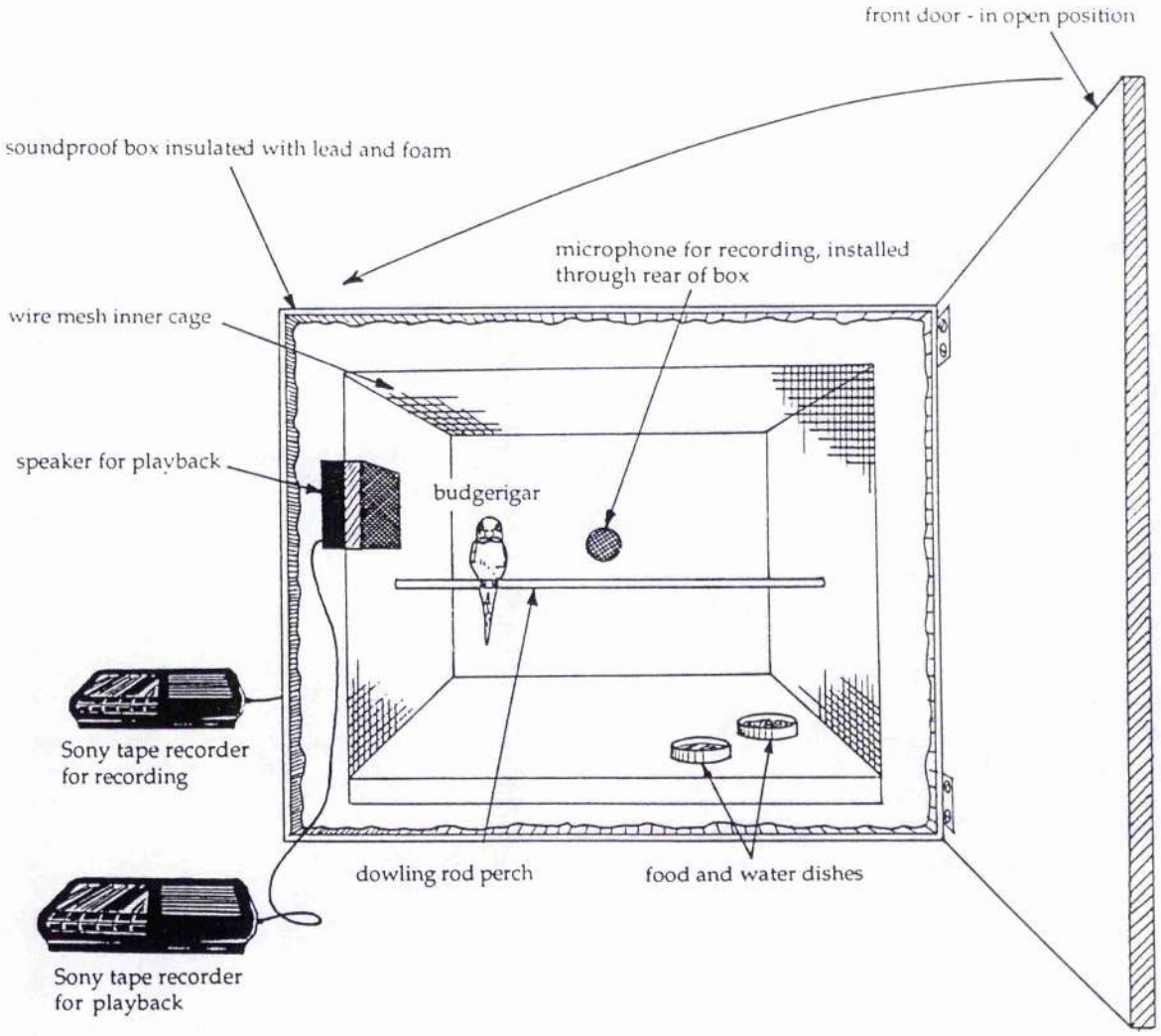


Figure 5.2 Soundproof box in which each budgerigar was housed for the 8 weeks of the study.

behaviours from each individual). Aggression on the other hand, often occurred very briefly and was therefore recorded as and when it happened. The behavioural categories recorded are summarised below.

Nearest neighbour

The nearest cagemate to each individual was recorded every 30 seconds. This measure was used as an assessment of proximity in preference to measuring absolute distances in units. Though absolute distances are more informative and easier to analyse statistically, they are often complicated to assess within a dynamic group of animals (Bartlett, 1993).

Aggressive displacements

As displacements were often brief and rarely prolonged, these interactions were recorded on a continuous basis, as and when they occurred. The individuals involved and the outcome of the interaction were noted (i.e. win, lose, or draw). All aggressive interactions were considered as one category (see Fig. 5.3A), despite there being three types, as follows:

- **displacement from perches**: bird A moves towards bird B, which is forced to give way.
- **beak fencing**: a physical interaction involving two birds 'jousting' on the perch by tapping beaks and pushing with breast feathers, usually resulting in one bird giving way. If no bird gives way, the context usually escalated to...
- **biting and wrestling**: an escalated aggressive interactions of the highest intensity, involving biting to the head, body and wings (sometimes resulting in wounds and loss of feathers) and rolling on the cage floor in a wrestling grasp.

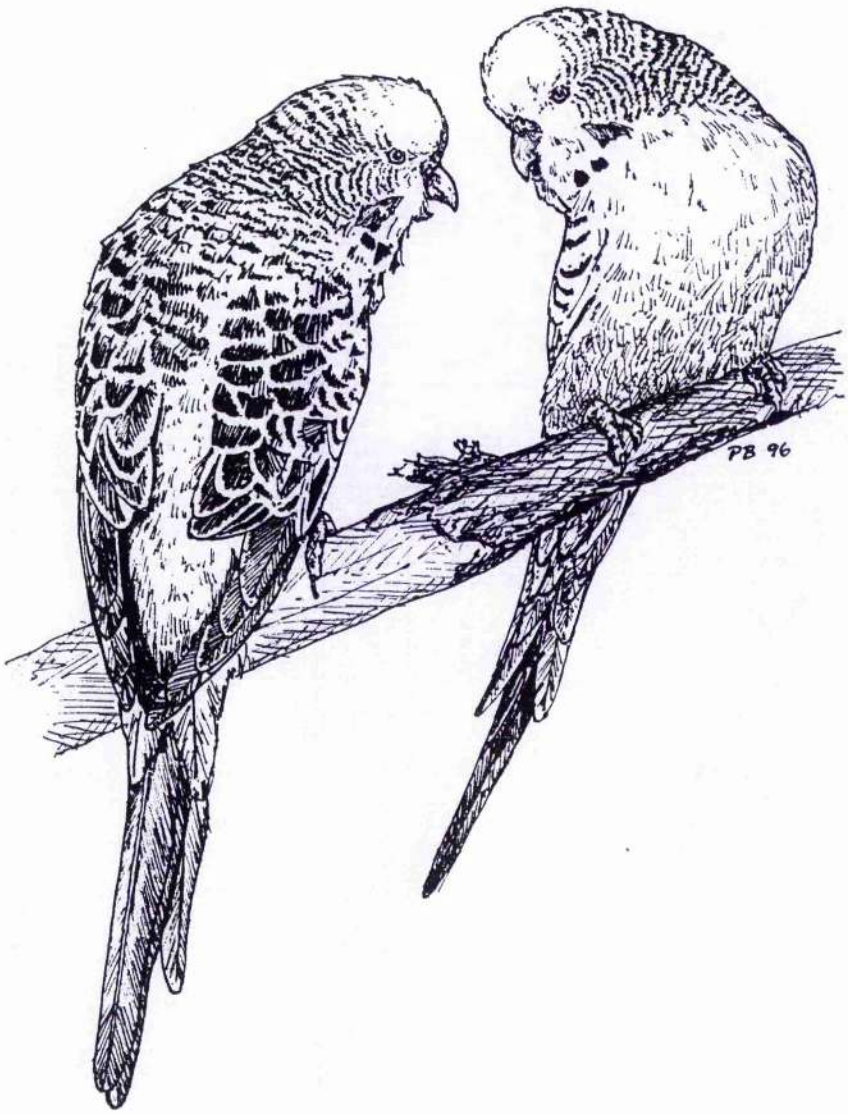


Fig. 5.3.A Budgerigars involved in an aggressive interaction, including biting, beak fencing and pushing with the body.

Preening and beak touching

For ease of analysis, both preening and beak touching were considered together; both behaviours are affiliative, serving to enhance bonds as well as a grooming function, and are often observed together during the same bout:

- *Preening (including allopreening)*: bird A preens bird B, usually around the head and neck regions, and bird B then returns the 'favour' to A. Sometimes A and B may preen one another simultaneously (see Fig. 5.3B).
- *Beak touching*: this is often observed during allopreening and involves both birds touching beaks and moving their heads downwards simultaneously, accompanied by a short 'squeek' call and contraction of the pupils of the eyes (see Fig. 5.3C). Preening would usually resume. This behaviour is most often seen between courting or mated pairs in a mixed flock (pers observ.)

The calling rate of each subject was also measured daily by playing-back conspecific calls and counting the number of calls in reply in a one minute period. This procedure was repeated for each bird in a randomized order with a quarter of an hour period in between to prevent a habituated response to the playback. There was no evidence to suggest that later playbacks gave less response with this interval. The calling rate would later be used in the analysis to determine whether birds that called more were more likely to be copied by the others, in preference to any social factors being important in the choice of 'tutor'.

5.2.4 Analysis of contact calls

Recordings of calls were firstly analysed by eye on the DSP Kay Digital Sonagraph to select the dominant calls of each individual, and to count the frequency with which these calls appeared.

Fig. 5.3.B A male budgerigar (right), distinguishable by its blue cere (nostrils), preening the head of its female mate.

Fig. 5.3.C Two male budgerigars involved in a duetting courtship interaction. Courting behaviour of this kind does occur frequently between males in the absence of any females. The grey male's pupils have contracted (indicating a highly aroused state), whilst the green male is adopting a submissive posture.

Comparisons of calls within and between individuals over the 10 weeks were made by cross-correlations of the spectrograms of the digitised recordings using Engineering Design's SIGNAL (version 3.0) software using cross-correlations of the digitised sonagrams along the time axis (using a Hanning window; sampling rate of 20 000 Hz; upper frequency limit of 8 kHz; Fast Fourier Transfer (FFT) size of 512; FFT interval of 13.2 sec; frequency resolution of 39.1 Hz; time resolution of 25.6 msec).

Cross-correlations were used to compare changes in call structure between and within individuals over the ten weeks of the study. Firstly recordings from each budgerigar were compared for each recording session (every four days), to detect whether there was a significant decrease in similarity with time from recordings of that individual at the start of the study, which would suggest that calls were changing in their characteristics over the duration of the study. The peak correlation values also give a measure of the extent of any change over a given period of time so that the rate of change can be assessed.

Comparisons were then made between each budgerigar's dominant calls within each group, at each four day point, to investigate whether individuals' calls were becoming more similar over time, i.e. to detect whether call convergence was occurring. Finally the results of the call comparisons were correlated with the behavioural data to detect whether any social factors were important in influencing the direction and extent of call convergence through mutual imitation.

5.3. Results

5.3.1. Cross-correlations

Pairwise cross correlations of sonagrams of calls were performed between all individuals in each group, at each 4 day interval. The peak correlation values (PCVs)

resulting from each cross correlation are shown in Figures 5.1.1.-5.1.6, 5.2.1.-5.2.6., and 5.3.1.-5.3.6. for groups 1, 2 and 3 respectively.

The graphs all show that the PCVs between all pairs of individuals were higher at the end of the study than at the start, indicating that the calls were more similar after the 53 days. Some birds, such as Lumo and John, John and Sam, Jack and Show, and Jesse and Ralph, showed dramatic increases in similarity over a fairly short period. Other pairs, such as John and Paddy, Bluey and Show, and Pied and Ralph, appeared to have copied each other to a lesser extent.

Statistical analysis of the PCVs in Figures 5.1.1.-5.3.6. were carried out using the bootstrap technique. Cross-correlations had initially been carried out between the calls of two individuals and a PCV obtained for each pair comparison, which was a measure of their similarity. Bootstrap analysis was then carried out between the PCVs of two birds with the PCVs of another two birds in order to determine whether any pair of individuals were more similar in the characteristics of their calls than any other pairs. For example, the mean PCV of Lumo and John (a measure of how similar their calls were) were compared by 500 bootstraps with the mean PCV of Lumo and Sam (see Table 5.1.1.). The result of 2.24 is above the value of 1.96 for P=0.05, and therefore we conclude that the sample with the highest mean, in this case Lumo and John, is significantly higher than Lumo and Sam. In otherwords, Lumo and John were more similar in their calls than Lumo and Sam.

Tables 5.1.1.-5.1.3. show the z-score results of bootstrapping between the PCVs of pairs of individuals as above. Any values in excess of 2.58 (P=0.01) show a significant difference between pairs in their similarity. In group 1, Lumo was most similar to John and Sam, whereas John, Sam and Paddy were equally most similar to all other cagemates. In group 2, Jack, Gigolo and Bluey were most similar to Show, and Show was most similar to Jack and Gigolo than to Bluey. In group 3, Ralph's call was more

Fig. 5.1.1. Lumo & John

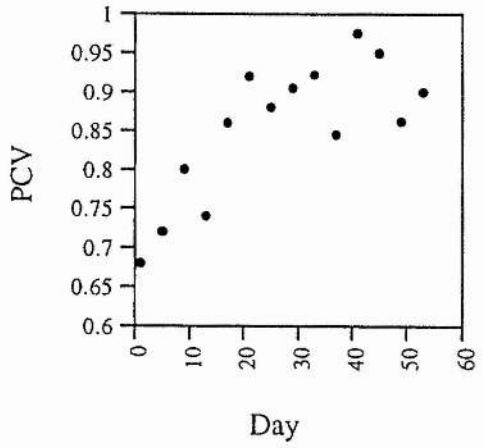


Fig.5.1.2. Lumo & Sam

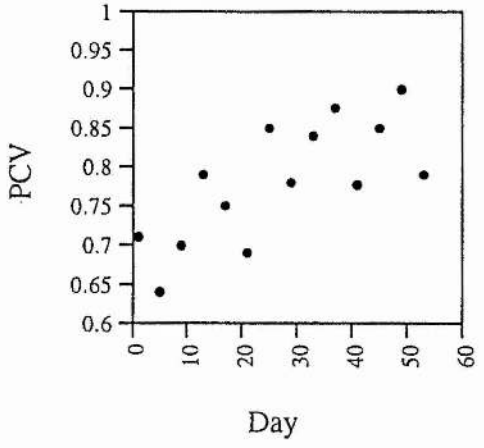


Fig. 5.1.3. Lumo & Paddy

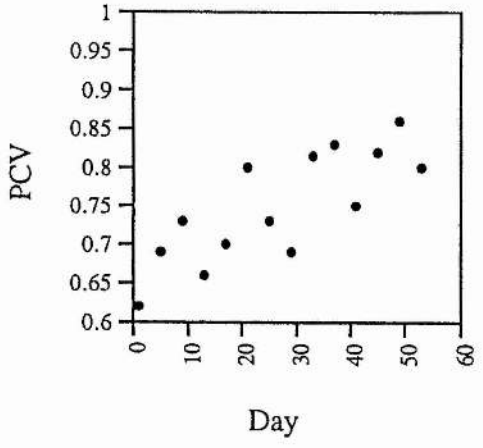


Fig. 5.1.4. John & Sam

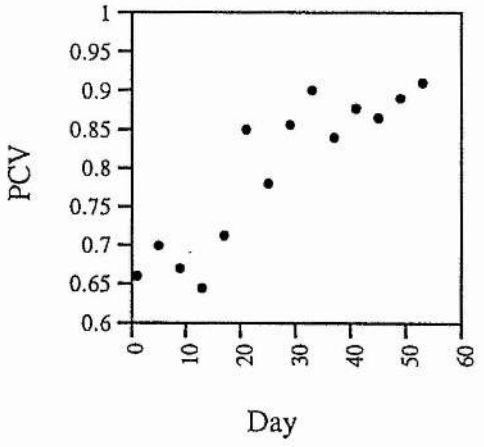


Fig. 5.1.5. John & Paddy

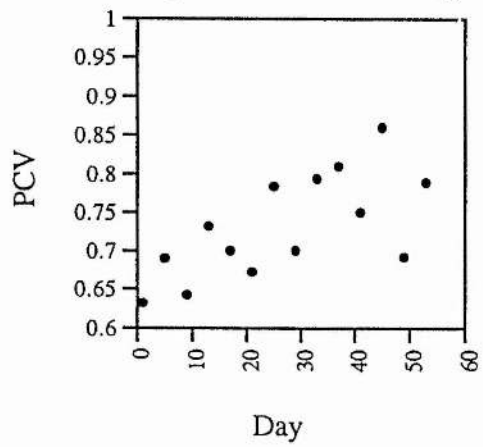


Fig. 5.1.6. Paddy & Sam

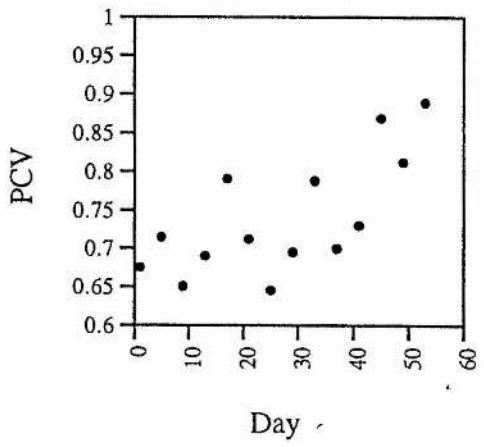


Fig. 5.1.1.- 5.1.6. Peak correlation values (PCV) for pairs of budgerigars over the duration of the study, resulting from cross-correlation comparisons of spectrograms of their calls.

Fig. 5.2.1. Jack & Bluey

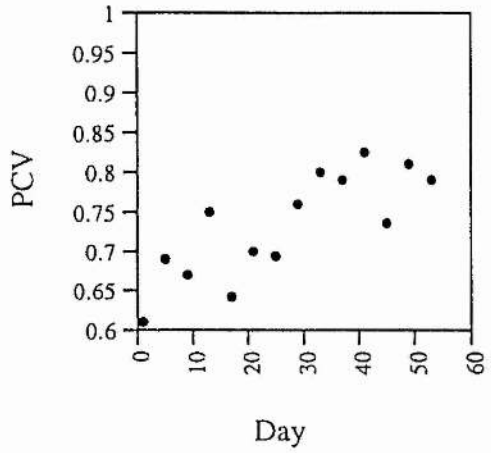


Fig. 5.2.2.Jack & Show

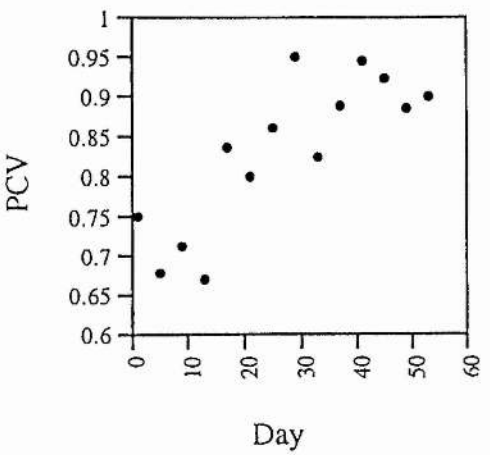


Fig. 5.2.3. Jack & Gigolo

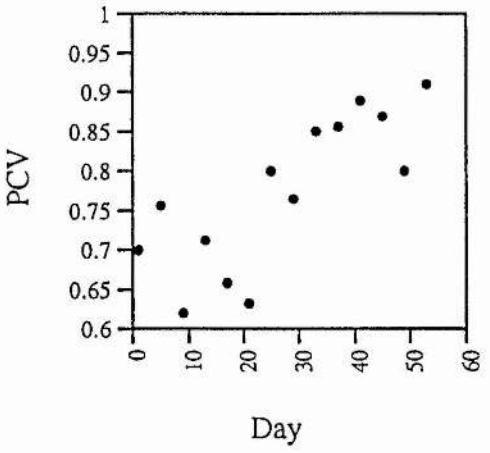


Fig. 5.2.4. Gigolo & Bluey

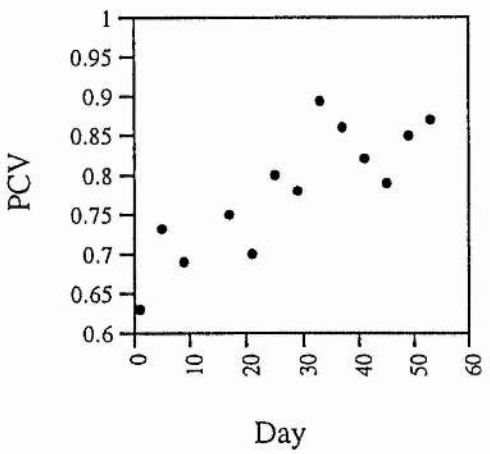


Fig. 5.2.5. Gigolo & Show

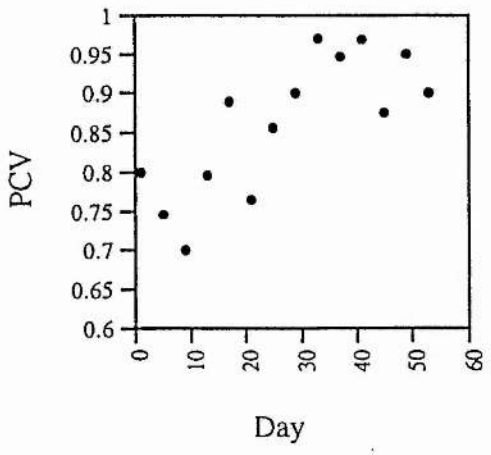


Fig. 5.2.6. Bluey & Show

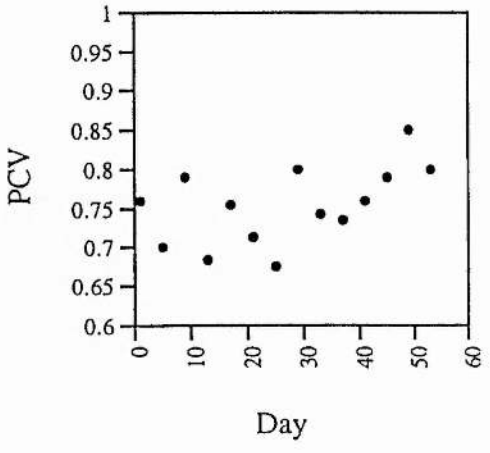


Fig. 5.2.1.- 5.2.6. Peak correlation values (PCV) for pairs of budgerigars in group 2 over the duration of the study, resulting from cross-correlation comparisons of spectrograms of their calls.

Fig. 5.3.1. Ben & Pied

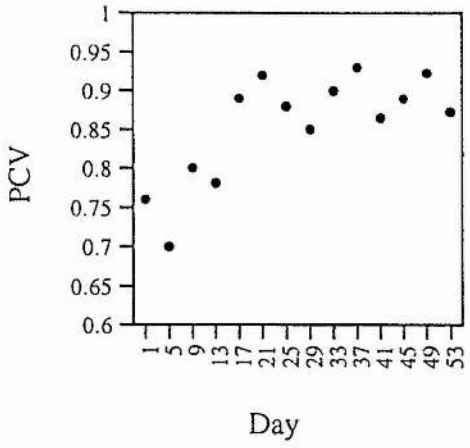


Fig. 5.3.2. Jesse & Ralph

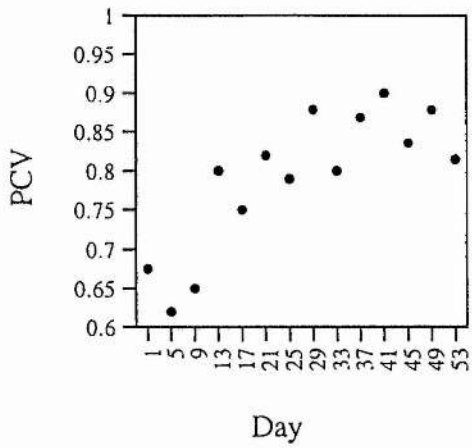


Fig. 5.3.3. Ben & Jesse

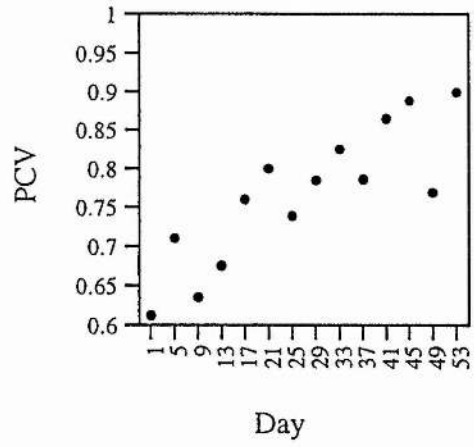


Fig. 5.3.4. Ben & Ralph

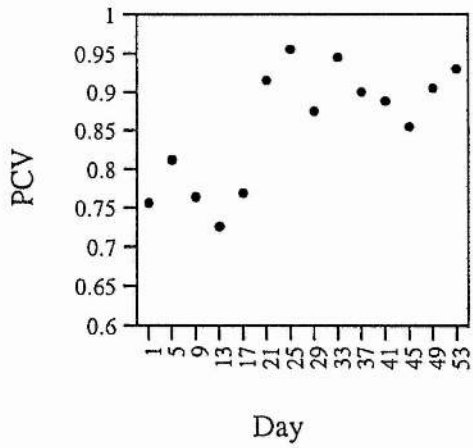


Fig. 5.3.5. Pied & Ralph

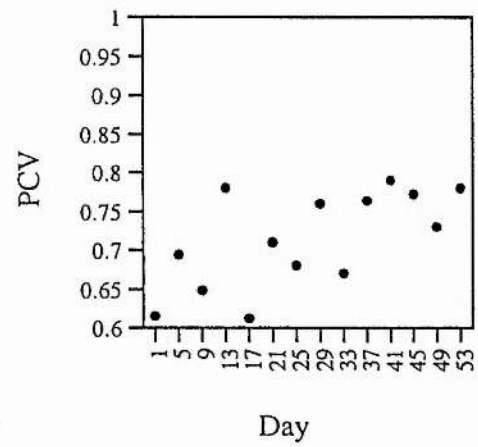


Fig. 5.3.6. Pied & Jesse

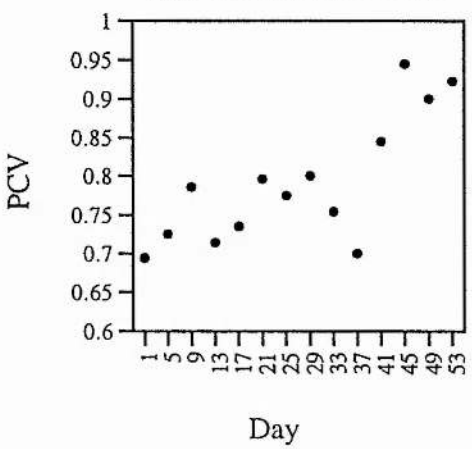


Fig. 5.3.1.- 5.3.6. Peak correlation values (PCV) for pairs of budgerigars in group 3 over the duration of the study, resulting from cross-correlation comparisons of spectrograms of their calls.

Pair comparisons	z-score	significance (P<0.01)
Lumo/John & Lumo/Sam	2.24	difference
Lumo/John & Lumo/Paddy	3.21	difference
Lumo/Sam & Lumo/Paddy	1.01	none
Lumo/Sam & John/Sam	0.43	none
Lumo/Sam & Paddy/Sam	1.37	none
John/Sam & Paddy/Sam	2.23	none
John/Sam & Lumo/John	1.26	none
John/Sam & Paddy/John	2.28	none
Paddy/John & Lumo/John	2.55	none
Paddy/Sam & Lumo/Paddy	0.35	none
Paddy/Sam & John/Paddy	0.32	none
Lumo/Paddy & John/Paddy	0.60	none

Table. 5.1.1. Z-score results from 500 bootstrap comparisons of the mean peak correlation values between pairs of individuals in group 1. The PCVs were obtained from cross-correlations of sonagrams of calls. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the PCVs of pairs.

Pair comparisons	z-score	significance (P<0.01)
Jack/Bluey & Jack/Show	2.42	none
Jack/Bluey & Jack Gigolo	0.79	none
Jack/Show & Jack/Gigolo	2.08	none
Jack/Gigolo & Gigolo/Bluey	0.12	none
Gigolo/Show & Gigolo/Bluey	2.34	none
Jack/Gigolo & Gigolo/Show	2.38	none
Jack/Show & Bluey/Show	2.68	difference
Jack/Show & Gigolo/Show	1.18	none
Bluey/Show & Gigolo/Show	3.63	difference
Jack/Bluey & Gigolo/Bluey	0.99	none
Jack/Bluey & Bluey/Show	0.29	none
Gigolo/Bluey & Bluey/Show	0.53	none

Table 5.1.2. Z-score results from 500 bootstrap comparisons of the mean peak correlation values between pairs of individuals in group 2. The PCVs were obtained from cross-correlations of sonagrams of calls. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the PCVs of pairs.

Pair comparisons	z-score	significance (P<0.01)
Ben/Pied & Ben/Ralph	0.33	none
Ben/Pied & Ben/Jesse	2.09	none
Ben/Ralph & Ben/Jesse	2.53	none
Jesse/Ralph & Ben/Jesse	0.63	none
Jesse/Ralph & Pied/Jesse	0.06	none
Ben/Jesse & Pied/Jesse	0.88	none
Jesse/Ralph & Ben/Ralph	2.05	none
Jesse/Ralph & Pied/Ralph	2.40	none
Ben/Ralph & Pied/Ralph	3.70	**difference**
Ben/Pied & Pied/Ralph	3.89	**difference**
Ben/Pied & Pied/Jesse	1.97	none
Pied/Ralph & Pied/Jesse	2.31	none

Table 5.1.3. Z-score results from 500 bootstrap comparisons of the mean peak correlation values between pairs of individuals in group 3. The PCVs were obtained from cross-correlations of sonagrams of calls. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the PCVs of pairs.

closely matched to Ben's than Jesse's, but was more similar to Jesse's than Pied's call; Ben, Pied, and Jesse were not more closely matched to any of their cagemates.

A quantifiable method of assessing which pairs of individuals copied each other most was devised by using a simple index based on PCV values. A value was obtained for the change in the PCV by subtracting the mean of the first four recording sessions from the mean of the last four for each pair. This represented how much the similarity between the two birds' calls had increased over the duration of the study and was referred to as the 'change in PCV'. The 'initial PCV' was the value of the first four recording sessions and this represented the actual similarity between two pairs before the 8 weeks of the study. From these two values a percentage change in the call was calculated:

$$\text{Percentage change in call} = \frac{\text{mean final PCV - mean initial PCV}}{\text{mean initial PCV}} \times 100$$

Figures 5.4.1., 5.4.2. and 5.4.3. show each pair of individuals' percentage change. Pairs with a higher percentage change in the call were judged to have copied each other more than those with lower values. For instance, in group 1, John and Sam clearly showed the greatest extent of copying, with Lumo and John also being good imitators of one anothers' calls. In group 2 Jack and Show were the pair that imitated each other most closely, while in group 3 it was Ben and Jesse. This method also took account of the fact that some birds were coincidentally closer in the characteristics of their call before the experiment was commenced, and could therefore have been misjudged to have copied more with different measures.

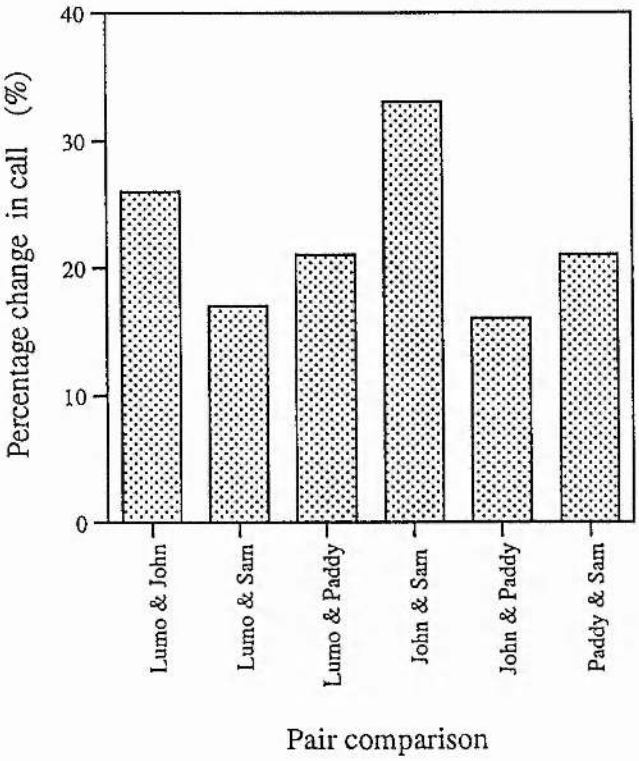


Fig. 5.4.1. Percentage change in call similarity between pairs of budgerigars in group 1 for the study as a whole. Call similarity between individuals was assessed by cross-correlations of spectrograms of the calls.

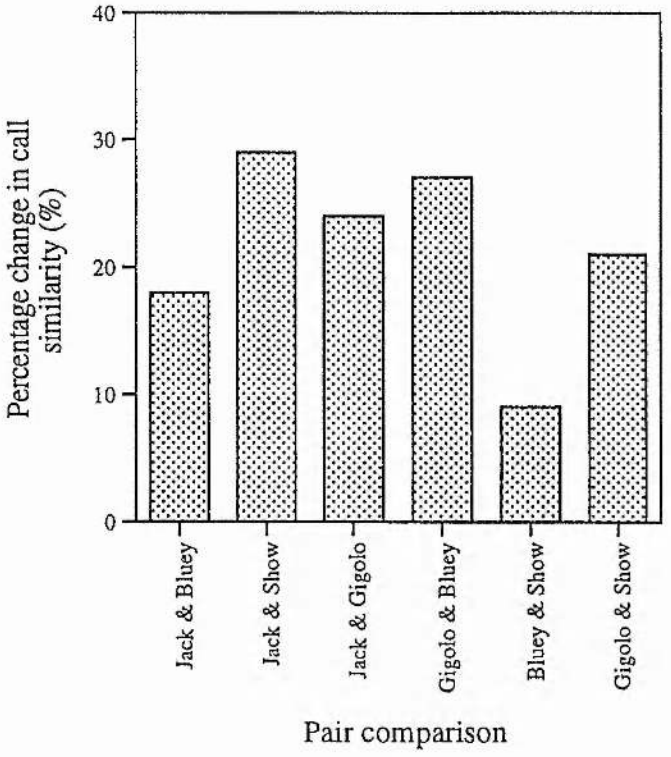


Fig. 5.4.2. Percentage change in call similarity between pairs of budgerigars in group 2 for the study as a whole. Call similarity between individuals was assessed by cross-correlations of spectrograms of the calls.

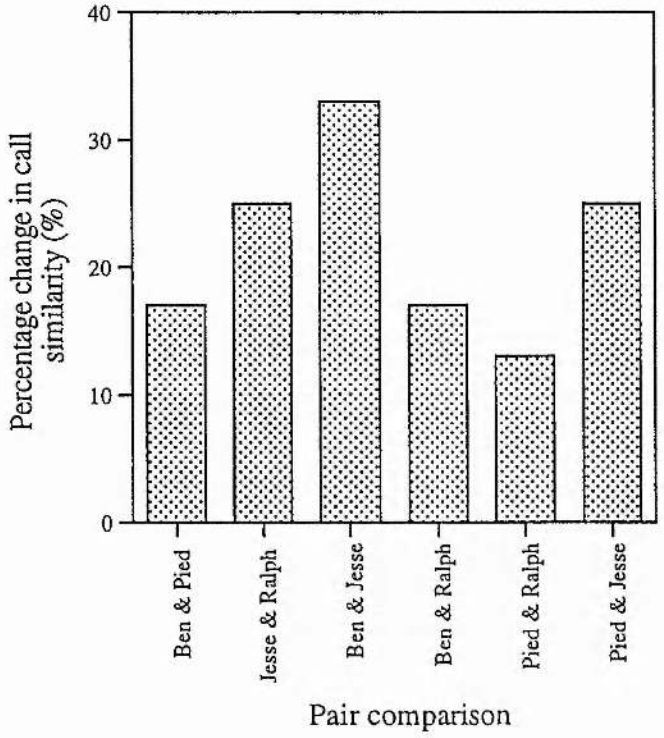


Fig. 5.4.3. Percentage change in call similarity between pairs of budgerigars in group 3 for the study as a whole. Call similarity between individuals was assessed by cross-correlations of spectrograms of the calls.

5.3.2. Proximity

The proximity between cagemates was measured as the proportion of time spent as the nearest neighbour to a particular individual. Figures 5.6.1.-5.6.3. show this, for each paired combination of birds, as a percentage of the total observed time over the whole duration of the study for each group.

Tables 5.2.1.-5.2.3. show the resulting z-score values from performing 500 bootstrap comparisons between the pairs shown in Figs. 5.6.1.-5.6.3. The proximity between two birds was initially measured (see fig. 5.6.1.-5.6.3.), and bootstrapping was performed between these values to compare whether certain individuals spent more time in proximity with each other than other pairs. For example, in table 5.2.1., the proximity between Lumo and John was compared with that between Lumo and Sam, and a z-score of 5.54 resulted from 500 bootstraps. This means that there was a significance difference between the pairs in their proximity, and from the higher mean value for Lumo and John we can say that John spent a significantly greater amount of time as nearest neighbour to Lumo than Sam.

In Table 5.2.1., any bootstrap comparisons that resulted in a significant z-score (i.e. above 2.58 for P=0.01) either involved Lumo and John or Paddy and Sam, which shows that these pairs were significantly more proximate to each other than any others in group 1.

Referring to Figs. 5.6.1.-5.6.3. and the statistical analysis of this data in Tables 5.2.1.-5.2.3., there are several clear trends which emerge. In group 1, most pairs were equally proximate to each other (between 25-30% of the time), except Lumo and John (44% of the time spent as nearest neighbours) and Paddy and Sam (35% of time as nearest neighbours). In group 2 it was most notably Jack and Gigolo that were significantly closer to each other for the most time (38%), and in group 3 it was Ben and Pied (39% of observed time as nearest neighbours).

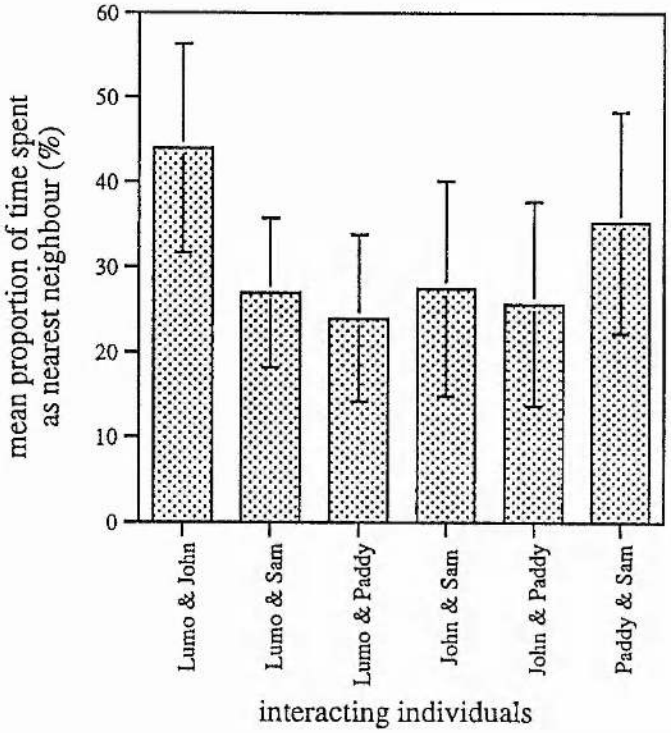


Fig. 5.6.1. The mean proportion of the total observed time that an individual was seen to be nearest neighbour to another specific cagemate in group 1. The error bars shown are standard deviations.

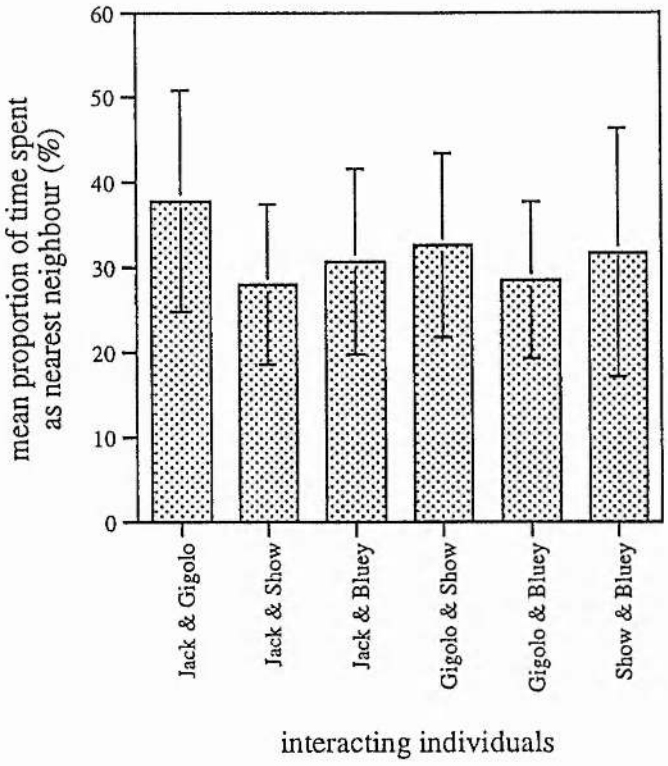


Fig. 5.6.2. The mean proportion of the total observed time that an individual was seen to be nearest neighbour to another specific cagemate in group 2. The error bars shown are standard deviations.

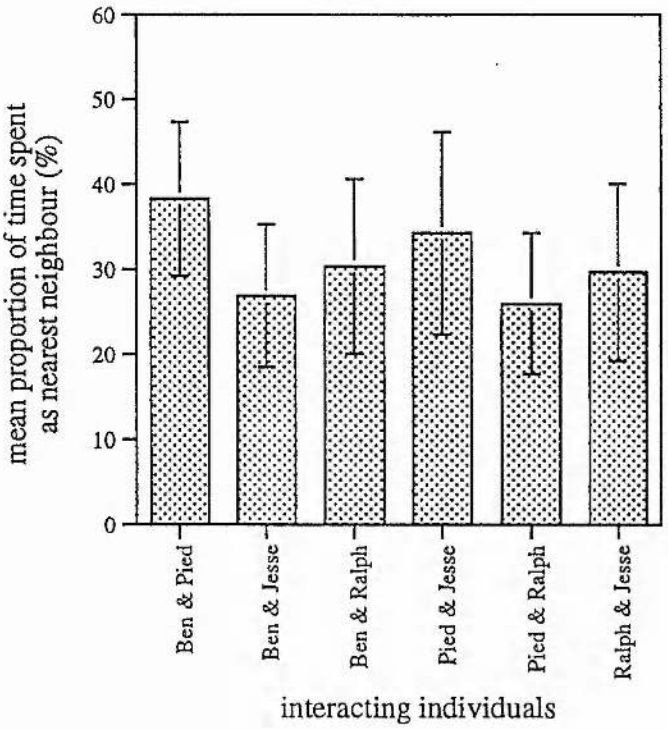


Fig. 5.6.3. The mean proportion of the total observed time that an individual was seen to be nearest neighbour to another specific cagemate in group 3. The error bars shown are standard deviations.

Pair comparisons	z-score	significance (P<0.01)
Lumo/John & Lumo/Sam	**5.54**	**difference**
Lumo/John & Lumo/Paddy	**6.15**	**difference**
Lumo/Sam & Lumo/Paddy	1.01	none
Lumo/Sam & John/Sam	0.13	none
Lumo/Sam & Paddy/Sam	**3.28**	**difference**
John/Sam & Paddy/Sam	**2.18**	none
John/Sam & Lumo/John	**4.80**	**difference**
John/Sam & Paddy/John	0.54	none
Paddy/John & Lumo/John	**5.50**	**difference**
Paddy/Sam & Lumo/Paddy	**3.85**	**difference**
Paddy/Sam & John/Paddy	**3.46**	**difference**
Lumo/Paddy & John/Paddy	0.59	none

Table. 5.2.1. Z-score results from 500 bootstrap comparisons of the mean proximity values between pairs of individuals in group 1. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the proximity of pairs.

Pair comparisons	z-score	significance (P≤0.01)
Jack/Bluey & Jack/Show	1.16	none
Jack/Bluey & Jack/Gigolo	**2.59**	**difference**
Jack/Show & Jack/Gigolo	**4.04**	**difference**
Jack/Gigolo & Gigolo/Bluey	**3.40**	**difference**
Gigolo/Show & Gigolo/Bluey	1.91	none
Jack/Gigolo & Gigolo/Show	2.08	none
Jack/Show & Bluey/Show	1.25	none
Jack/Show & Gigolo/Show	**1.98**	none
Bluey/Show & Gigolo/Show	0.25	none
Jack/Bluey & Gigolo/Bluey	0.91	none
Jack/Bluey & Bluey/Show	0.24	none
Gigolo/Bluey & Bluey/Show	1.03	none

Table 5.2.2. Z-score results from 500 bootstrap comparisons of the mean proximity values between pairs of individuals in group 2. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the proximity of pairs.

Pair comparisons	z-score	significance (P<0.01)
Ben/Pied & Ben/Ralph	3.05	difference
Ben/Pied & Ben/Jesse	5.19	difference
Ben/Ralph & Ben/Jesse	1.69	none
Jesse/Ralph & Ben/Jesse	1.19	none
Jesse/Ralph & Pied/Jesse	1.49	none
Ben/Jesse & Pied/Jesse	2.99	difference
Jesse/Ralph & Ben/Ralph	0.22	none
Jesse/Ralph & Pied/Ralph	1.74	none
Ben/Ralph & Pied/Ralph	2.11	none
Ben/Pied & Pied/Ralph	5.29	difference
Ben/Pied & Pied/Jesse	1.44	none
Pied/Ralph & Pied/Jesse	3.70	difference

Table 5.2.3. Z-score results from 500 bootstrap comparisons of the mean proximity values between pairs of individuals in group 3. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the proximity ot pairs.

The proximity of pairs of individuals between the first and last four weeks of the study was compared with a Wilcoxon text. Some pairs showed a significant increase in their proximity; Paddy and Sam ($T=68.5$, $N=23$, $P<0.05$), Jack and Bluey ($T=63$, $N=23$, $P<0.05$), Gigolo and Bluey ($T=55$, $N=23$, $P<0.02$). Jack and Gigolo showed a significant decrease in their proximity over the study period ($T=71$, $N=23$, $P<0.05$).

5.3.3. Preening

The number of preening interactions between individuals showed decidedly more variation than the proximity data. Figures 5.8.1.-5.8.3. illustrate the mean number of preenings per observation period for the whole of the eight week study.

The results of the statistical bootstrap analysis on these data are shown in Tables 5.4.1.-5.4.3. The z-scores indicate that most pairs are significantly different in terms of the number of preening interactions that they share. Some pairs, such as Lumo and John and Ben and Ralph, indulge in relatively frequent preenings (approximately 4 per observation period), whereas others, Lumo and Paddy and Pied and Ralph, only preen each other on average less than once every observation period. One pair, Jack and Bluey, were not observed to preen each other for the first half of the study, and only once in every two observation sessions thereafter.

It is also interesting to note that the number of preenings shown by an individual varies substantially depending on the preening partner concerned. For instance, in group 1, Lumo was involved in almost 4 interactions per day with John, 2 with Sam and about once every two observation periods with Paddy. This would tend to suggest a preference for mutual preening with John over the other cagemates. If, on the other hand, Lumo's preening frequencies had been consistently high with all individuals, then we could conclude that this bird was a 'frequent preener' without showing any tendency for preference with one partner or another.

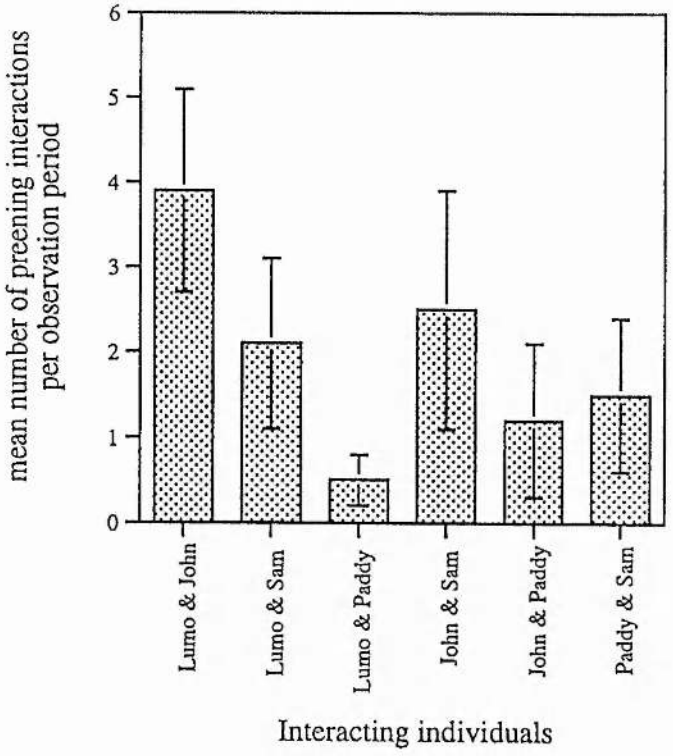


Fig. 5.8.1. The mean number of occassions for the study as a whole when two individuals were seen to be preening each other per observation period in group 1. Interquartiles are shown.

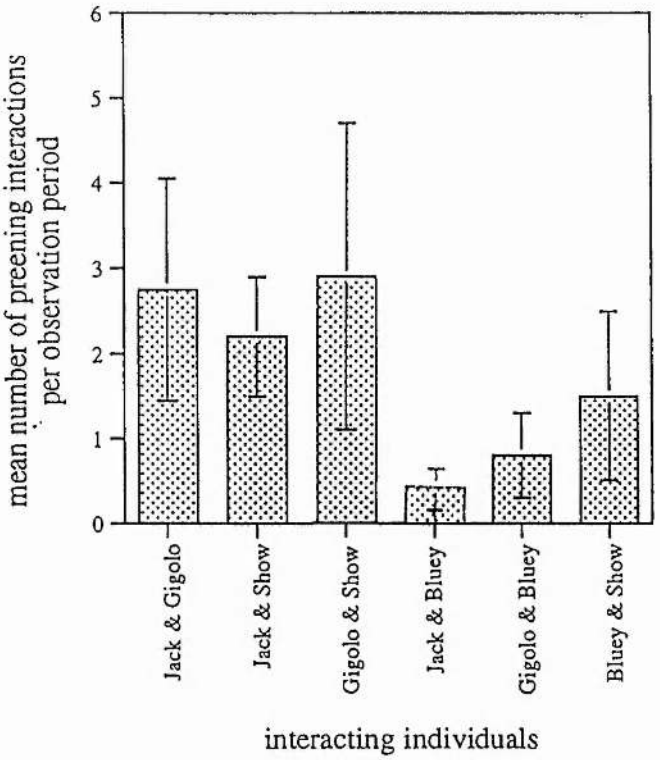


Fig. 5.8.2. The mean number of occassions for the study as a whole when two individuals were seen to be preening each other per observation period in group 2. Interquartiles are shown.

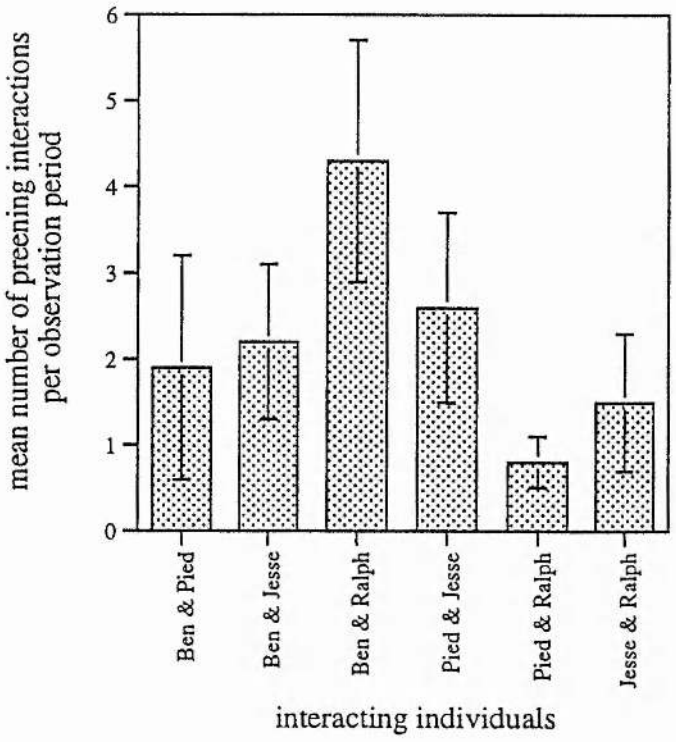


Fig. 5.8.3. The mean number of occasions for the study as a whole when two individuals were seen to be preening each other per observation period in group 3. Interquartiles are shown.

Pair comparisons	z-score	significance (P<0.01)
Lumo/John & Lumo/Sam	4.89	difference
Lumo/John & Lumo/Paddy	8.95	difference
Lumo/Sam & Lumo/Paddy	5.95	difference
Lumo/Sam & John/Sam	2.50	none
Lumo/Sam & Paddy/Sam	3.08	difference
John/Sam & Paddy/Sam	4.63	difference
John/Sam & Lumo/John	4.02	difference
John/Sam & Paddy/John	6.33	difference
Paddy/John & Lumo/John	5.15	difference
Paddy/Sam & Lumo/Paddy	3.73	difference
Paddy/Sam & John/Paddy	1.45	none
Lumo/Paddy & John/Paddy	3 26	difference

Table 5.4.1. Z-score results from 500 bootstrap comparisons of the mean number of preening interactions between pairs of budgerigars in group 1. Z-scores equal or above 2.58 (P=0.01) indicate a significant difference between the two samples.

Pair comparisons	z-score	significance (P<0.01)
Jack/Bluey & Jack/Show	5.47	difference
Jack/Bluey & Jack/Gigolo	7.52	difference
Jack/Show & Jack/Gigolo	1.98	none
Jack/Gigolo & Gigolo/Bluey	4.79	difference
Gigolo/Show & Gigolo/Bluey	6.55	difference
Jack/Gigolo & Gigolo/Show	1.09	none
Jack/Show & Bluey/Show	3.11	difference
Jack/Show & Gigolo/Show	2.90	difference
Bluey/Show & Gigolo/Show	4.63	difference
Jack/Bluey & Gigolo/Bluey	2.58	difference
Jack/Bluey & Bluey/Show	3.67	difference
Gigolo/Bluey & Bluey/Show	2.94	difference

Table 5.4.2. Z-score results from 500 bootstrap comparisons of the mean number of preening interactions between pairs of individuals in group 2. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference.

Pair comparisons	z-score	significance (P<0.01)
Ben/Pied & Ben/Ralph	8.56	difference
Ben/Pied & Ben/Jesse	1.23	none
Ben/Ralph & Ben/Jesse	6.88	difference
Jesse/Ralph & Ben/Jesse	3.51	difference
Jesse/Ralph & Pied/Jesse	4.25	difference
Ben/Jesse & Pied/Jesse	2.66	difference
Jesse/Ralph & Ben/Ralph	6.28	difference
Jesse/Ralph & Pied/Ralph	3.39	difference
Ben/Ralph & Pied/Ralph	8.36	difference
Ben/Pied & Pied/Ralph	4.40	difference
Ben/Pied & Pied/Jesse	2.85	difference
Pied/Ralph & Pied/Jesse	5.16	difference

Table 5.4.3. Z-score results from 500 bootstrap comparisons of the mean number of preening interactions between pairs of individuals in group 3. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference.

Fig. 5.9 shows the mean number of preenings per observation period during the first and the last half of the study, for all three groups. Comparing these figures between the first half and the last half of the study with the Wilcoxon test showed that there was no significant change in the number of preenings between pairs over the study duration, for the groups as a whole.

However, on an individual pair basis, there did appear to be some increases and decreases in preening between specific pairs (see Fig. 5.10.1-5.10.3). Wilcoxon tests for each pair between the first and last half of the study, revealed that some pairs did indulge in more significant preening in the second half of the study; Lumo and Sam ($T=47$, $N=23$, $P<0.02$), John and Sam ($T=21$, $N=23$, $P<0.002$), Jack and Bluey ($T=12.5$, $N=23$, $P<0.002$); Bluey and Show ($T=19$, $N=23$, $P<0.002$), and Ben and Pied ($T=76$, $N=23$, $P<0.05$). Some pairs showed a significant decrease in their preening interactions in the last four weeks of the study; Jack and Show ($T=44$, $N=23$, $P<0.02$) and Pied and Ralph ($T=69$, $N=23$, $P<0.02$).

A Spearman Rank Correlation Coefficient between the mean number of preenings in the first half of the study, and the difference between the mean preening of the first and last half of the study (i.e. the increase or decrease in preening) showed that there was no significant correlation ($r_s = 0.103$), and thus no tendency for high or low preening pairs at the start of the study, to increase or decrease more over the duration of the study.

5.3.4. Calling rates

The calling rates of all individuals in each group were measured daily, and the means for the study as a whole are shown in Figures 5.11.1., 5.11.2. and 5.11.3. for groups 1 to 3 respectively.

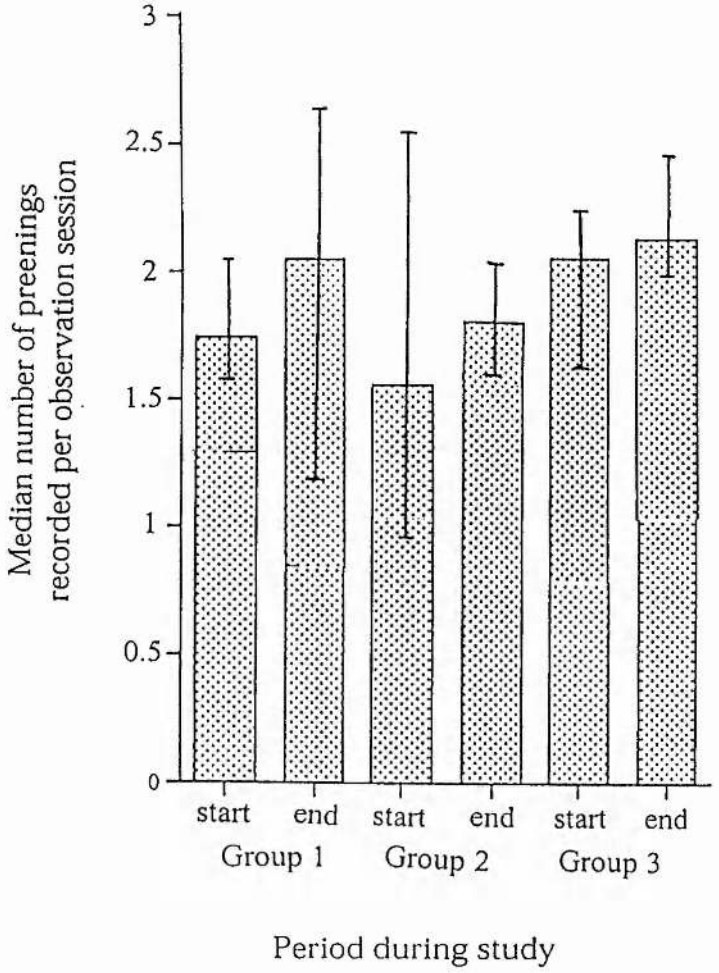


Fig. 5.9 Comparison between the median number of preening interactions recorded per observation session during the first half (start) and last half (end) of the study for pairs of individuals in Groups 1-3. Interquartiles are shown.

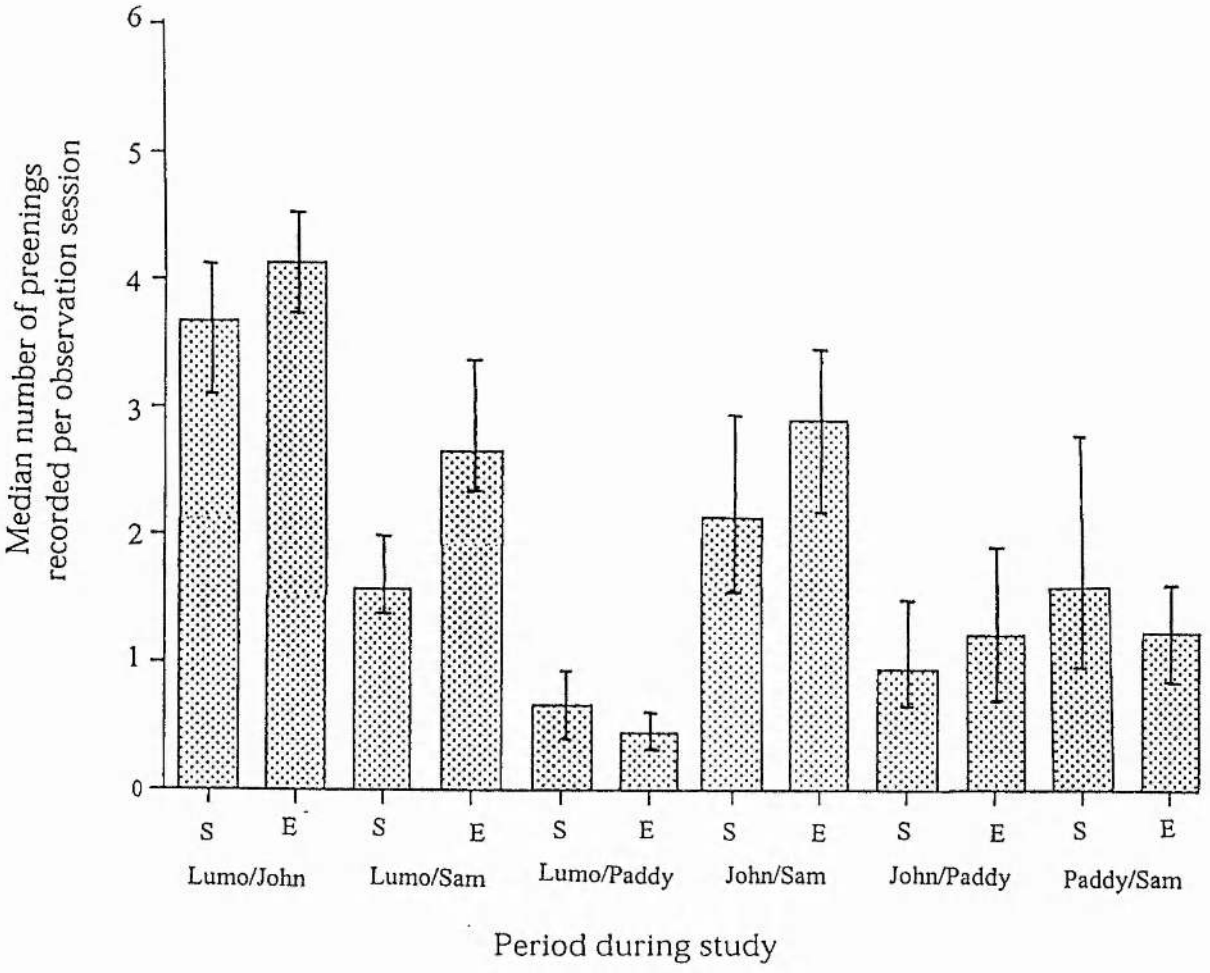


Fig. 5.10.1 Comparison between the median number of preening interactions recorded per observation session during the first half (S) and last half (E) of the study for pairs of individuals in Group 1. Interquartiles are shown.

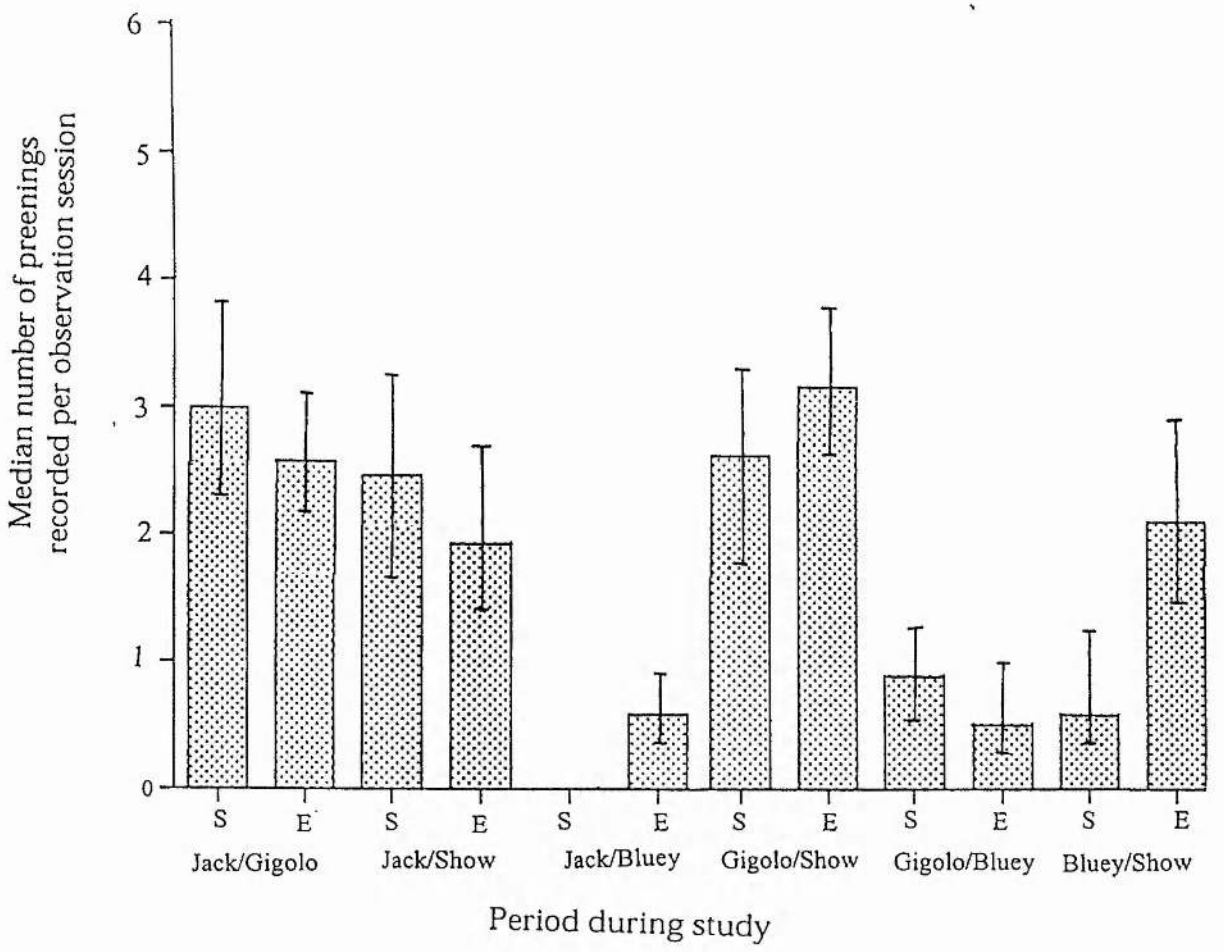


Fig. 5.10.2 Comparison between the median number of preening interactions recorded per observation session during the first half (S) and last half (E) of the study for pairs of individuals in Group 2. Interquartiles are shown.

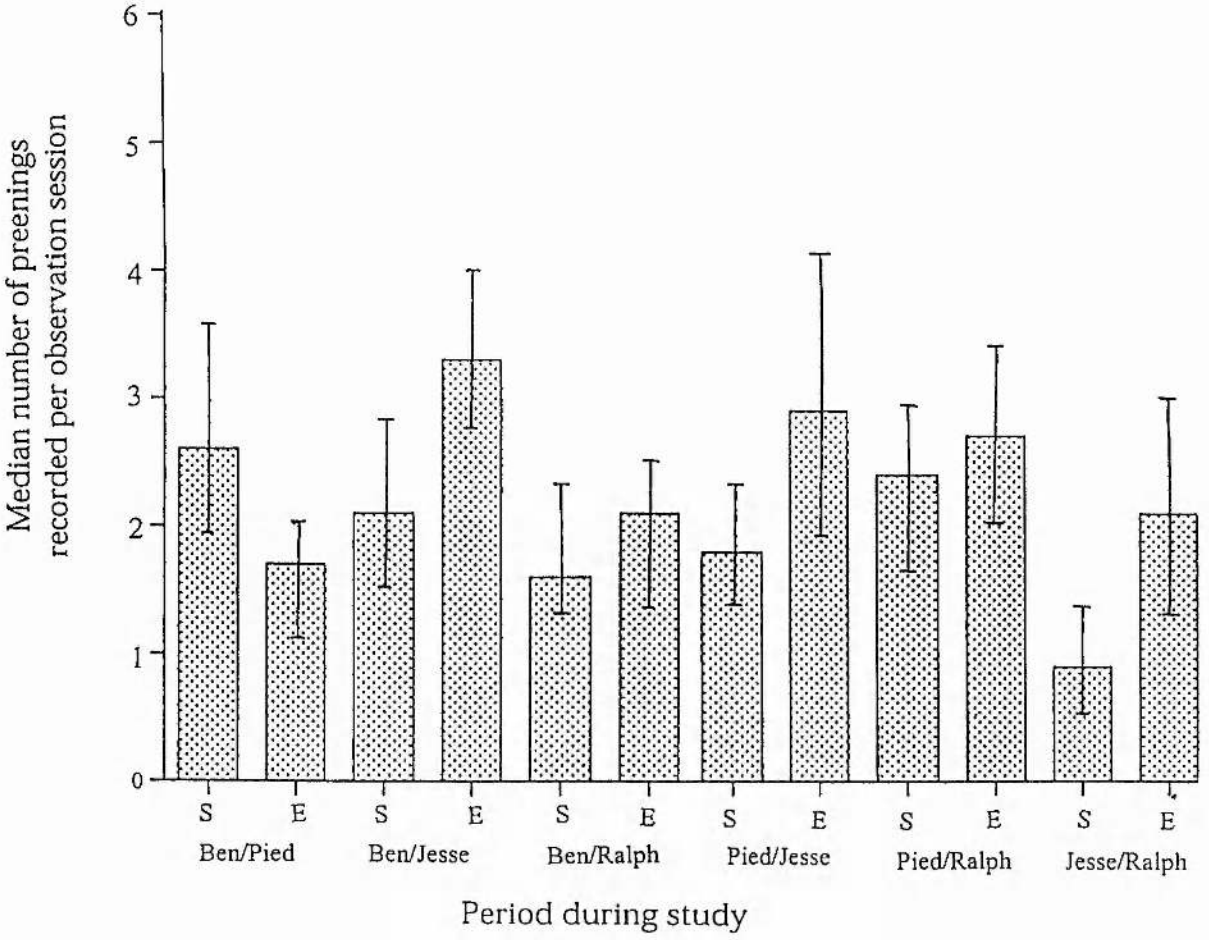


Fig. 5.10.3 Comparison between the median number of preening interactions recorded per observation session during the first half (S) and last half (E) of the study for pairs of individuals in Group 3. Interquartiles are shown.

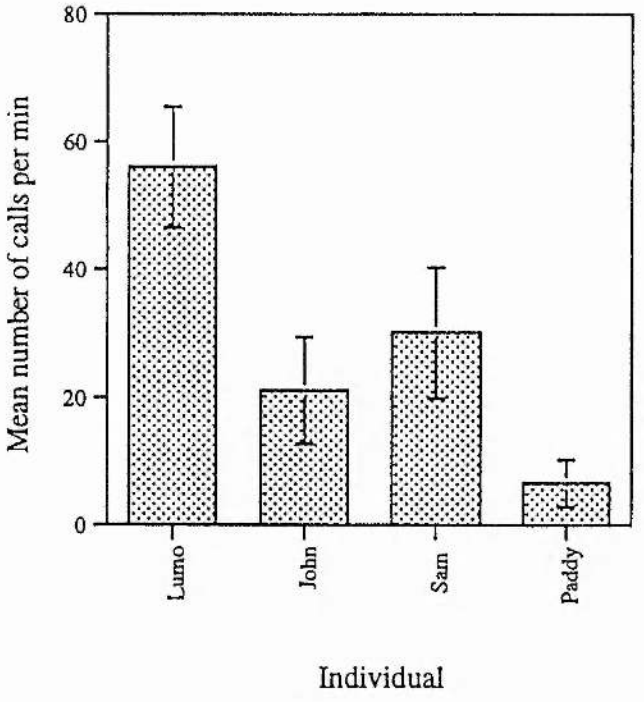


Fig. 5.11.1 The median of the study as a whole for the number of calls given per minute by individuals in group 1. Interquartiles are shown.

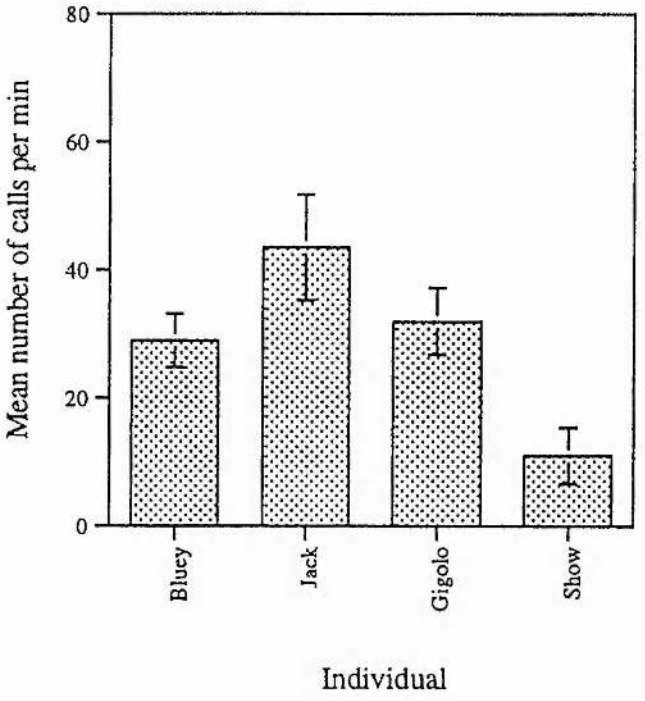


Fig. 5.11.2 The median of the study as a whole for the number of calls given per minute by individuals in group 2. Interquartiles are shown.

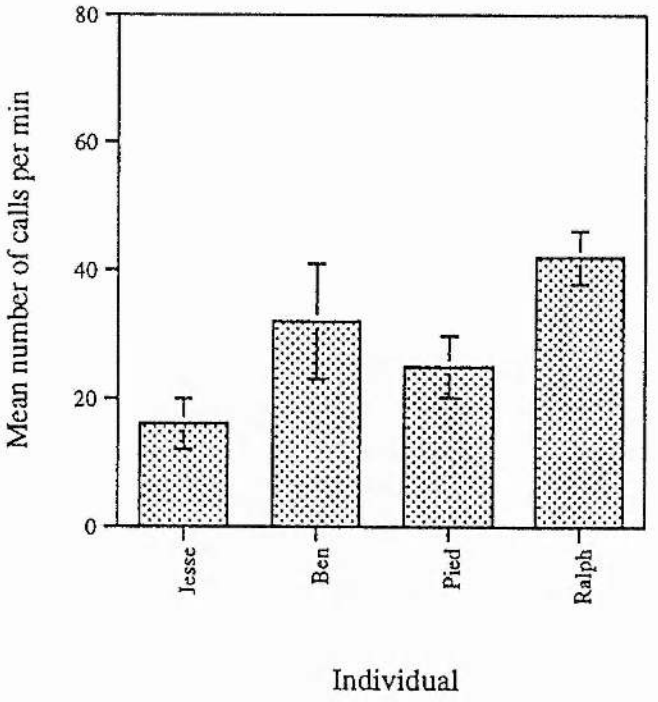


Fig. 5.11.3 The median of the study as a whole for the number of calls given per minute by individuals in group 3. Interquartiles are shown.

It is apparent from Figures 5.11.1.-5.11.3. that each budgerigar tends to have a fairly distinctive rate of calling with the intra-individual difference between successive days being fairly small compared to differences between individuals. Kruskal-Wallis tests for each group revealed the differences between individuals to be highly significant at $P<0.01$ for all three groups (Group 1: $H = 156.43$, $df = 3$; Group 2: $H = 132.84$, $df = 3$; Group 3: $H = 98.83$, $df = 3$).

In group 1 in particular, Lumo proved to call at a consistently high rate (mean for whole experiment = 56 calls min^{-1}), whereas its cagemate Paddy would usually give around 7 calls in a minute. In group 2 it was Jack that would usually call most frequently (mean = 44 calls min^{-1}), and Show the least (mean = 11 calls min^{-1}), and in group 3, Ralph called the most (mean = 42 calls min^{-1}) whilst Jesse called the least (mean = 16 calls min^{-1}). Other individuals in each flock would call at intermediate levels within a range of approximately $\pm$ 10 calls min^{-1}.

The majority of individuals' call rates remained fairly consistent throughout the study, but some budgerigars showed a significant increase in calling rate. Wilcoxon's test for matched pairs revealed that Lumo ($W = 214.5$, $n = 18$, $P<0.01$), John ($W = 224.5$, $n = 18$, $P<0.01$), Gigolo ($W = 202$, $n = 18$, $P<0.05$) and Pied ($W = 196.5$, $n = 18$, $P<0.05$), all had higher calling rates in the last 4 weeks of the study compared to the first 4 weeks.

5.3.5. Aggression

Most birds showed no tendency to increase or decrease significantly the frequency of their directed aggression at the end of the study. The exception to this were Lumo and Paddy ($T=70.5$, $N=23$, $P<0.05$), and Paddy and Sam ($T=64.5$, $N=23$, $P<0.05$) in group 1, and Ben and Pied in group 3 ($T=52$, $N=23$, $P<0.02$), which were significantly less aggressive to each other during the second half of the eight week period.

The means of the data are shown in Figures 5.12.1.-5.12.3. for each pair, representing the degree of aggressiveness (see methods for measurement of aggression) between pairs for the study as a whole. Tables 5.6.1.-5.6.3. show the z-score results of bootstrap comparisons of these pairs, to determine whether there were any significant differences in the aggression observed between specific pairs of individuals.

In group 1, John was involved in significantly more interactions with Paddy and Lumo. In group 2, Jack and Gigolo were more aggressive to Bluey than any other cagemates, whereas Bluey was observed to be aggressive to Jack and Gigolo with equally high frequency. In group 3, it was Ralph that showed most aggression towards Ben, Pied, and Jesse, and similarly all three cagemates were involved to an equal extent in aggressive encounters with Ralph.

The proportion of aggressive interactions won was also calculated for each individual. Fig. 5.13.1-5.13.3 show the proportion as a percentage of the total number of aggressive encounters that each bird was involved in.

An assessment of the probable dominance hierarchy in each group is shown in Fig. 5.14.1-5.14.3. These dominance hierarchies are based on the rank ordering based on dyadic interactions according to who supplants whom (Appleby, 1983). The number of supplants between pairs are arranged in a matrix and the order has been arranged so that the individual that is last supplanted is at the top, and the one that is always supplanted is at the bottom.

The matrices give an indication of the extent of dominance of certain individuals in a group, but they also illustrate the non-linear nature of dominance in budgerigars. There are indeed, no instances when one individual completely dominates another and is never supplanted by this bird (as would be indicated by values of 0 in the matrix). All interactions between pairs involve some dominance reversals (A supplants B, and B

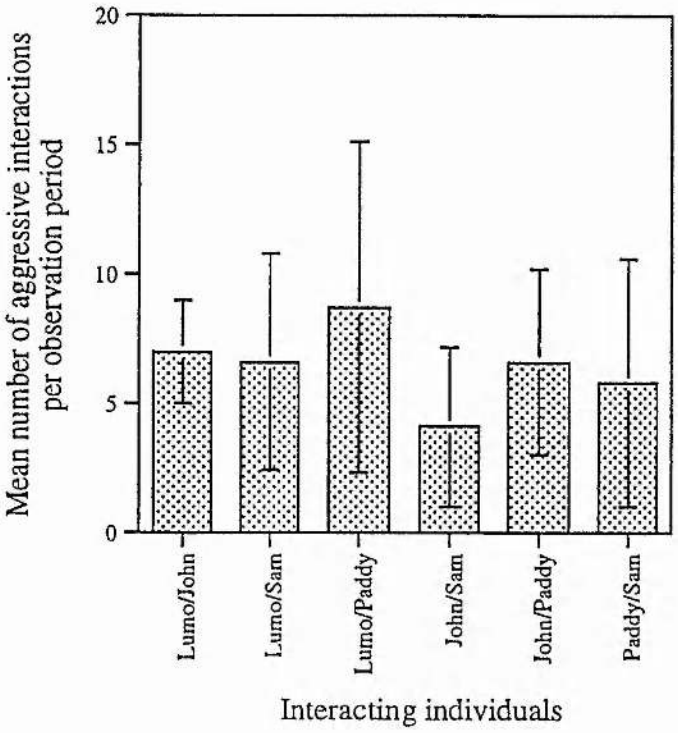


Fig. 5.12.1 The mean number of aggressive interaction between individuals in group 1 per observation period for the study as a whole. Standard deviations are shown.

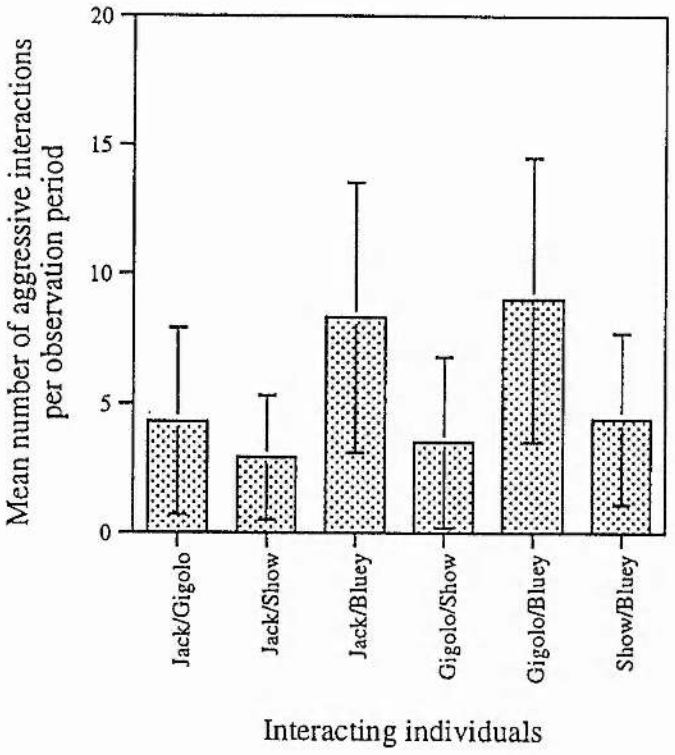


Fig. 5.12.2 The mean number of aggressive interactions between individuals in group 2 per observation period for the study as a whole. Standard deviations are shown.

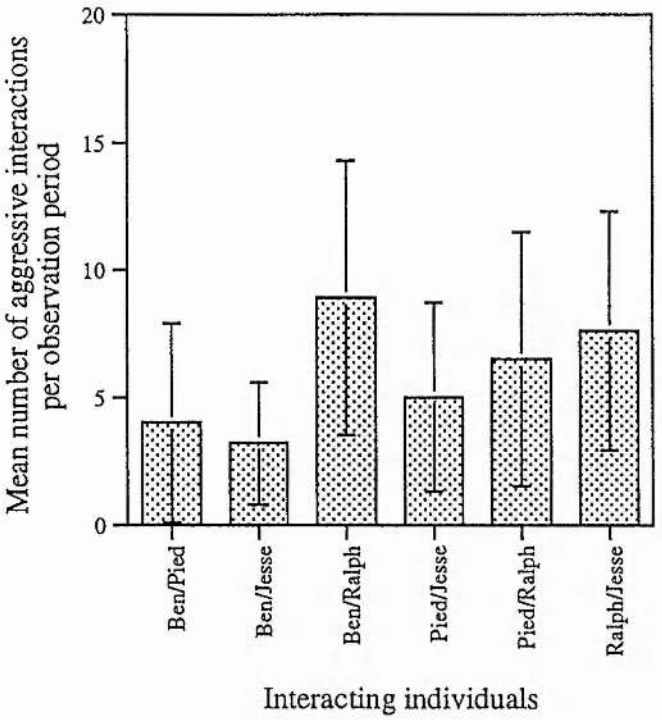


Fig. 5.12.3 The mean number of aggressive interaction between individuals in group 3 per observation period for the study as a whole. Standard deviations are shown.

Pair comparisons	z-score	significance (P<0.01)
Lumo/John & Lumo/Sam	0.48	none
Lumo/John & Lumo/Paddy	1.14	none
Lumo/Sam & Lumo/Paddy	1.17	none
Lumo/Sam & John/Sam	0.13	none
Lumo/Sam & Paddy/Sam	0.71	none
John/Sam & Paddy/Sam	1.81	none
John/Sam & Lumo/John	3.74	difference
John/Sam & Paddy/John	2.89	difference
Paddy/John & Lumo/John	0.85	none
Paddy/Sam & Lumo/Paddy	1.96	none
Paddy/Sam & John/Paddy	1.88	none
Lumo/Paddy & John/Paddy	1.51	none

Table. 5.6.1 Z-score results from 500 bootstrap comparisons of the mean number of aggressive interactions between pairs of individuals in group 1. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the aggressiveness of pairs.

Pair comparisons	z-score	significance (P<0.01)
Jack/Bluey & Jack/Show	5.02	difference
Jack/Bluey & Jack Gigolo	3.96	difference
Jack/Show & Jack/Gigolo	1.15	none
Jack/Gigolo & Gigolo/Bluey	4.00	difference
Gigolo/Show & Gigolo/Bluey	4.60	difference
Jack/Gigolo & Gigolo/Show	1.13	none
Jack/Show & Bluey/Show	2.33	none
Jack/Show & Gigolo/Show	1.40	none
Bluey/Show & Gigolo/Show	1.23	none
Jack/Bluey & Gigolo/Bluey	0.65	none
Jack/Bluey & Bluey/Show	3.73	difference
Gigolo/Bluey & Bluey/Show	4.04	difference

Table 5.6.2. Z-score results from 500 bootstrap comparisons of the mean number of aggressive interactions between pairs of individuals in group 2. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the aggressiveness of pairs.

Pair comparisons	z-score	significance (P<0.01)
Ben/Pied & Ben/Ralph	4.61	difference
Ben/Pied & Ben/Jesse	1.18	none
Ben/Ralph & Ben/Jesse	5.10	difference
Jesse/Ralph & Ben/Jesse	5.18	difference
Jesse/Ralph & Pied/Jesse	2.69	difference
Ben/Jesse & Pied/Jesse	2.51	none
Jesse/Ralph & Ben/Ralph	1.21	none
Jesse/Ralph & Pied/Ralph	0.94	none
Ben/Ralph & Pied/Ralph	1.71	none
Ben/Pied & Pied/Ralph	2.83	difference
Ben/Pied & Pied/Jesse	1.13	none
Pied/Ralph & Pied/Jesse	1.53	none

Table 5.6.3. Z-score results from 500 bootstrap comparisons of the mean number of aggressive interactions between pairs of individuals in group 3. Any z-scores above the threshold value of 2.58 for P=0.01 indicate a significant difference between the aggressiveness of pairs.

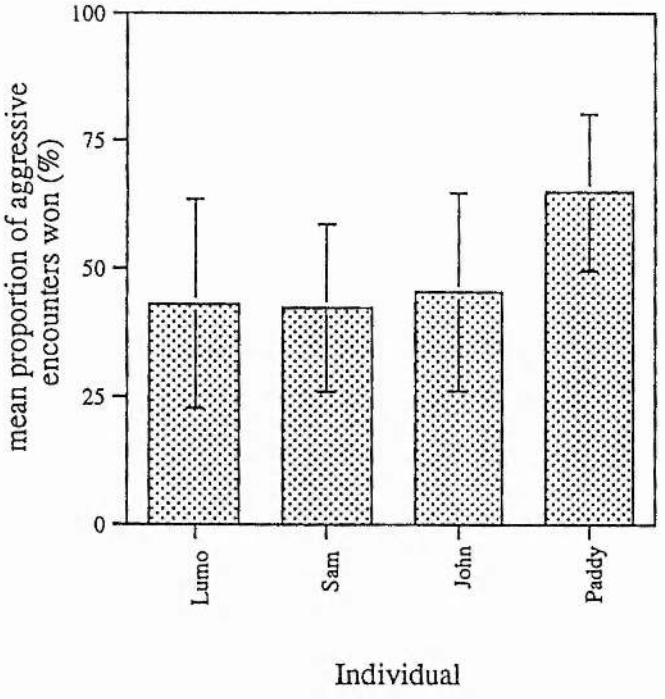


Fig. 5.13.1. The mean proportion of aggressive encounters won by each individual in group 1 for the study as a whole. Standard deviations are shown.

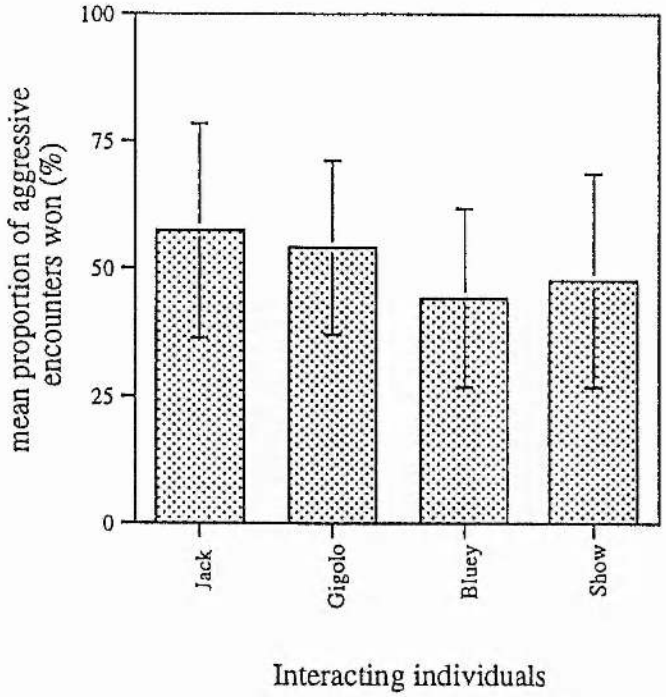


Fig. 5.13.2. The mean proportion of aggressive encounters won by each individual in group 2 for the study as a whole. Standard deviations are shown.

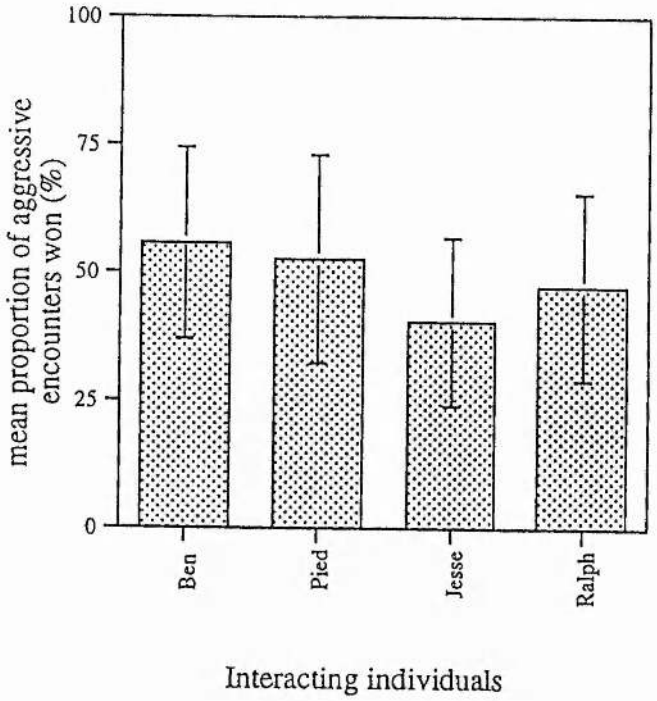


Fig. 5.13.3. The mean proportion of aggressive encounters won by each individual in group 3 for the study as a whole. Standard deviations are shown.

Figs 5.14: the dominance matrices showing the wins and losses for aggressive interactions between individuals in each group. Birds are ordered in rank of dominance with the most dominant positioned at the top and left of the matrix.

Fig. 5.14.1 Dominance matrix for group 1

NUMBER OF OCCASIONS WHEN INDIVIDUAL IS SUPPLANTED (LOSSES)

INDIVIDUAL SUPPLANTS (WINS)

	Paddy	Lumo	John	Sam
Paddy		45	25	57
Lumo	20		11	24
John	26	5		10
Sam	26	22	15	

Fig. 5.14.2 Dominance matrix for group 2

NUMBER OF OCCASIONS WHEN INDIVIDUAL IS SUPPLANTED (LOSSES)

INDIVIDUAL SUPPLANTS (WINS)

	Gigolo	Bluey	Jack	Show
Gigolo		17	6	13
Bluey	24		7	13
Jack	1	28		7
Show	9	12	13	

Fig. 5.14.3 Dominance matrix for group 3

NUMBER OF OCCASIONS WHEN INDIVIDUAL IS SUPPLANTED (LOSSES)

INDIVIDUAL SUPPLANTS (WINS)

	Ben	Pied	Jesse	Ralph
Ben		15	9	22
Pied	12		14	31
Jesse	9	6		32
Ralph	13	27	16	

supplants A). Calculation of Landau's index of linearity (*h*), reveals that none of the groups' dominance hierarchies are linear (Group 1, h=0.2; Group 2, h=0.2, and Group 3, h=0.6).

5.3.6. The relationship between call matching and social factors

The data from the social factors: aggressive interactions between individuals, proximity and preening, were correlated with each other and the degree of copying between individuals, to determine which factors were most influencial the degree of copying between certain cagemates.

Table 5.8 shows the results of Spearman Rank Correlation Coefficients between the three social factors and degree of copying (i.e. percentage change in similarity between two birds) for all three groups as a whole.

The degree of preening is significantly and positively correlated with the extent of copying and proximity. There is a strong correlation between the similarity of calls between individuals and the amount of mutual preening that each pair performs (r_S = 0.875, n = 18, P<0.01). There is also a significant modest correlation between the extent of preening and the proximity of a pair (r_S = 0.482, n = 18, P<0.05) which is perhaps not unexpected, considering individuals must be very close to preen one another.

So far, each social factor that was measured between individuals has been correlated with the extent of call matching to determine which has the greatest influence. The effect, if any, of the amount of calling by each individual and the number of aggressive encounters it won were also considered in relation to the total percentage change in call for each individual, refelecting how much an individual copied its cagemates. In this way, the influence of dominance and calling rate on tutor choice could be assessed.

Table 5.8 Spearman Rank Correlation Coefficients for correlations between social factors for all birds in all three groups (see text for full description).

	Change in PCV	Proximity	Aggression
Proximity	0.482*		
Aggression	0.351	- 0.270	
Preening	0.875**	0.487*	- 0.432

* significant at $P<0.05$
** significant at $P<0.01$

Table 5.9 Spearman Rank Correlation Coefficients for correlations between percentage change in the call, calling rate, and dominance for all birds in all three groups (see text for full description).

	Total % change in PCV	Calling rate
Calling rate	0.112	
Dominance score	- 0.390	0.028

The influence of a particular individual on the rest of its group was determined by adding its similarity scores for each of its three cagemates. This gave a value which quantified the total extent of call matching per individual. A correlation was then performed for all three groups as a whole, incorporating the 'extent of matching' value, call rate, and the dominance score (derived from the total number of times a bird supplanted all of its cagemates, subtracted by the total number of times a bird is supplanted), the results of which are shown in Table 5.9. None of the factors tested were significantly correlated with the extent of copying as measured by the total percentage change in call similarity. Therefore, birds that called more, and which were apparently more dominant, did not show any greater tendency to copy or be copied more.

5.3.7 Changes in the sonagrams of individuals' calls

Figs 5.15.1-5.15.3 represent sonagrams of the calls of budgerigars in groups 1, 2 and 3 respectively at the start and end of the study. Each individual's call in week 1 of the experiment was clearly different from its cagemates'. By week 8, without exception, all individuals in each group that were housed together, produced calls that were very similar in the pattern of frequency modulation and duration. There were no obvious similarities in the group specific call between experimental groups.

5.5. Discussion

The importance of social factors in the learning of conspecific vocalisations is widely known in many species of birds (Immelmann, 1969; Mundinger, 1979; Baptista & Petrinovich, 1984; Slater *et.al.*, 1988; Pepperberg, 1990). In chapter 4 of this thesis it was concluded that a social element was not vital for learning to occur, but was generally needed for accurate and complete copying in a social species such as the budgerigar.

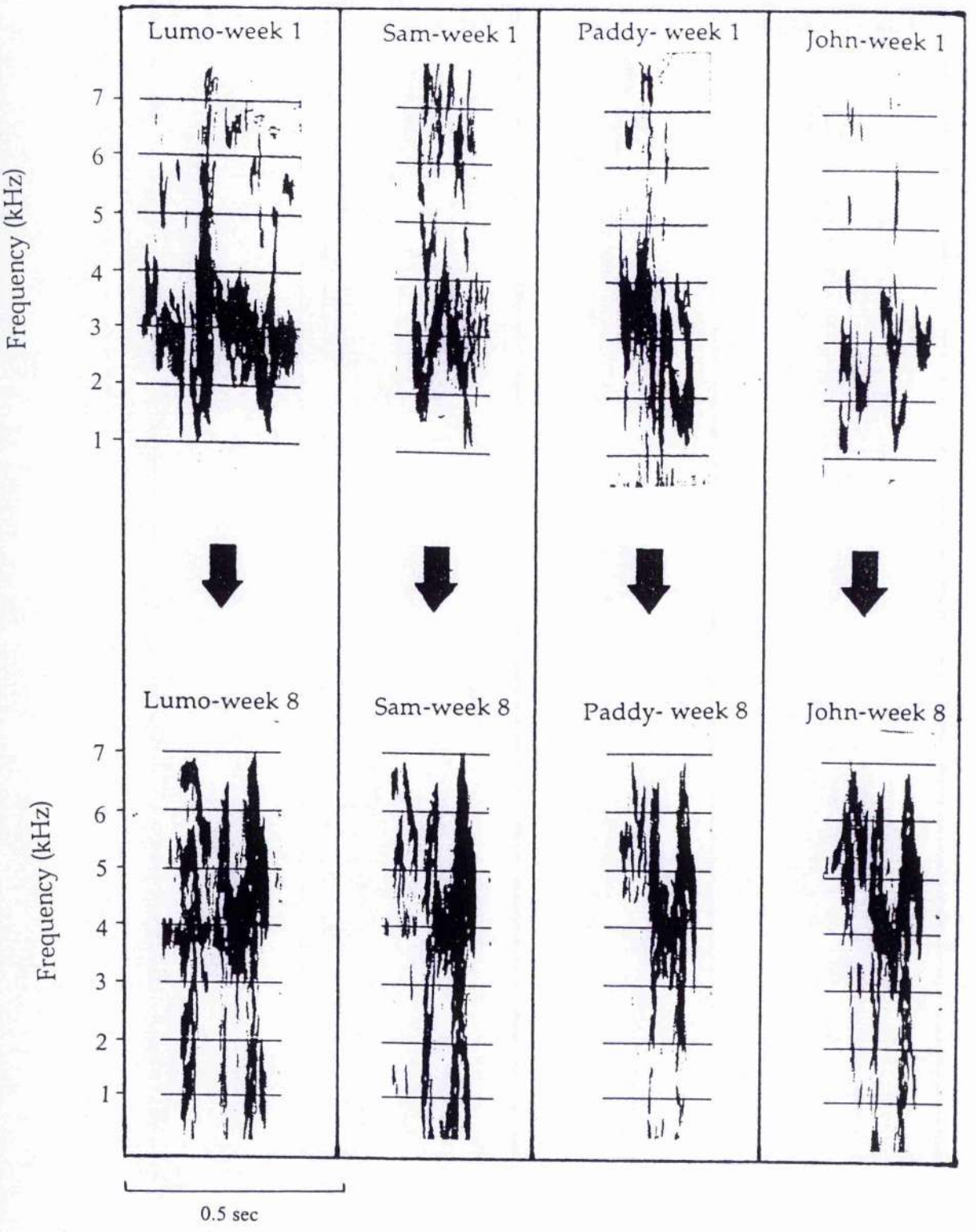


Fig. 5.15.1 Sonagrams of the dominant contact calls of individual budgerigars in group 1 during the start of the experiment (week 1) and the end (week 8).

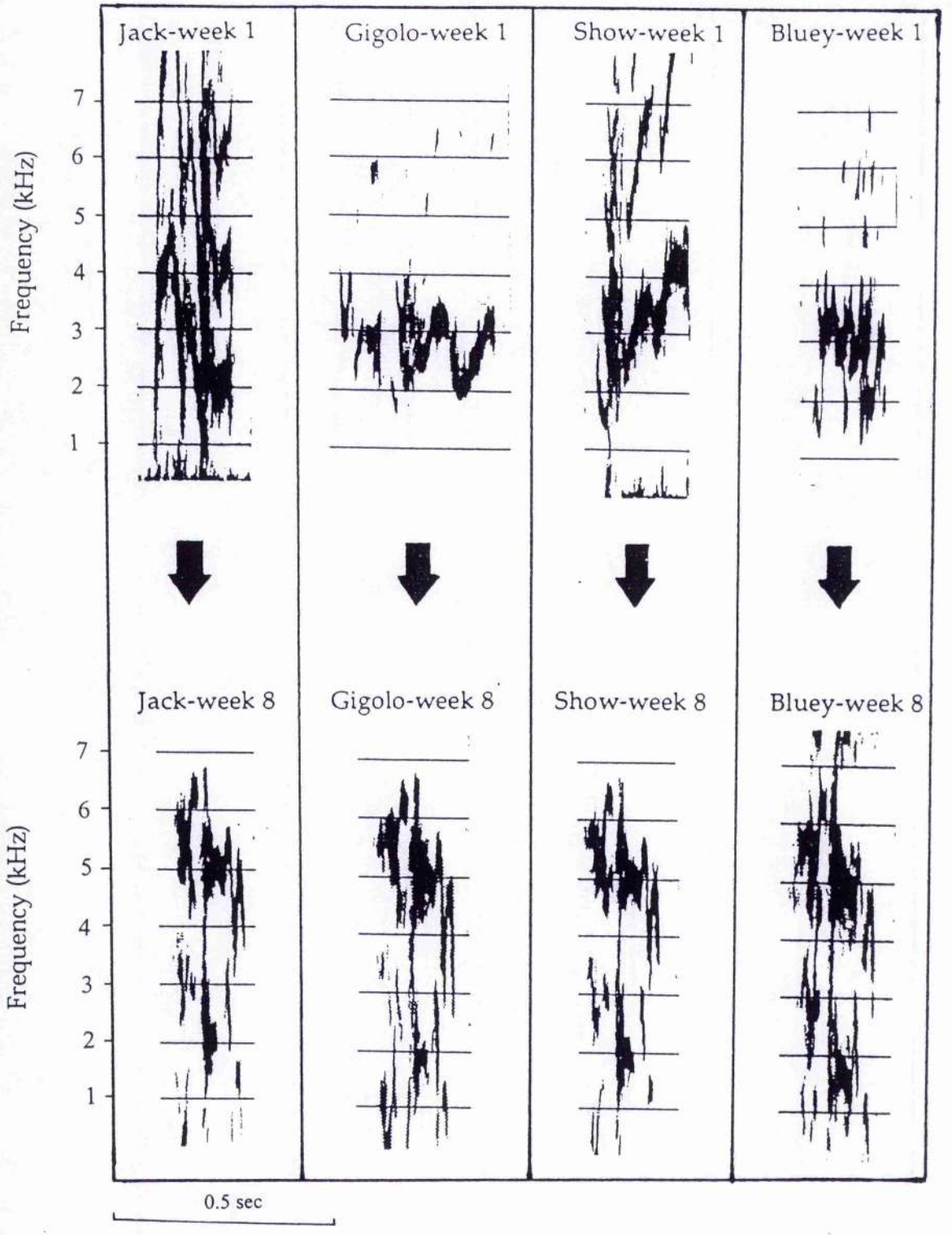


Fig. 5.15.2 Sonagrams of the dominant contact calls of individual budgerigars in group 2 during the start of the experiment (week 1) and the end (week 8).

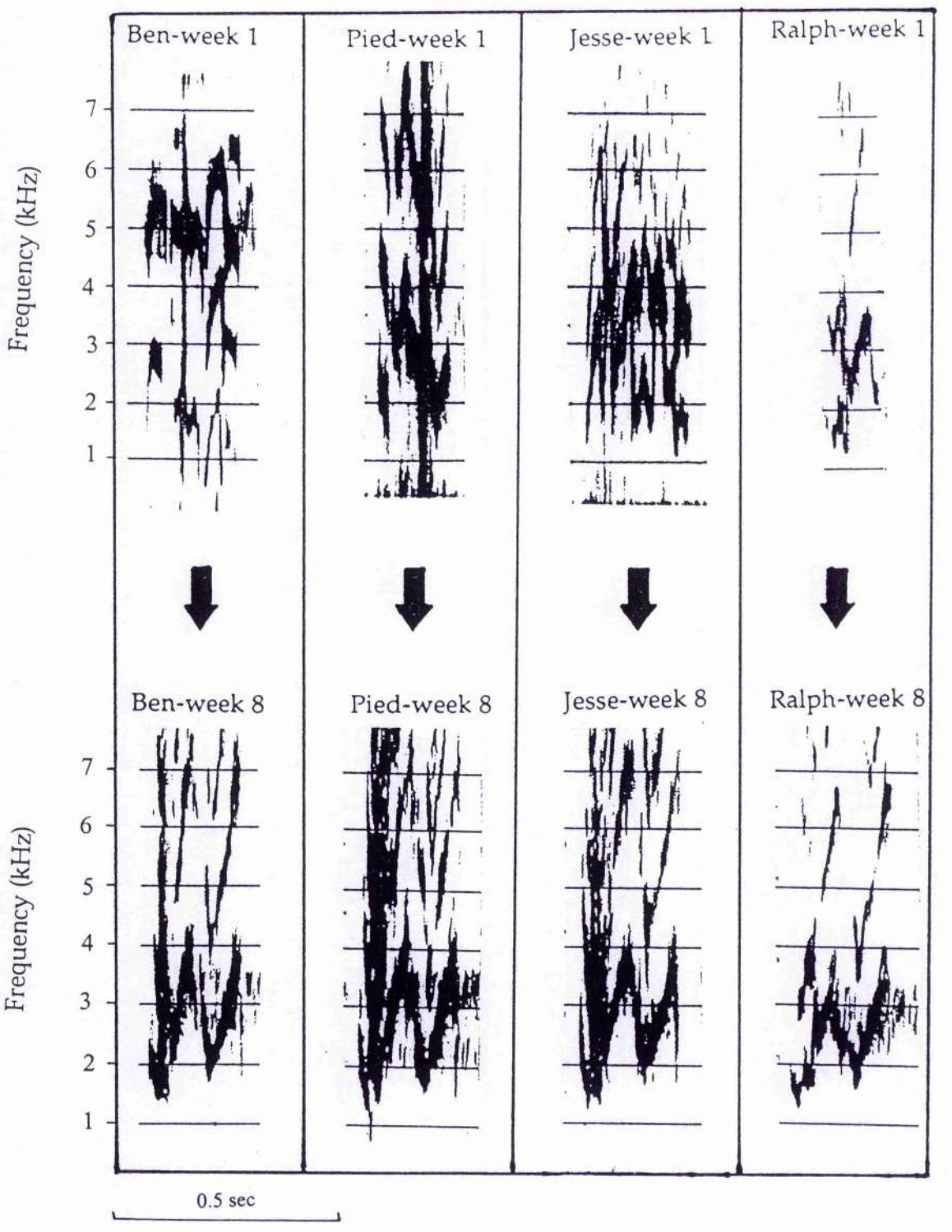


Fig. 5.15.3 Sonagrams of the dominant contact calls of individual budgerigars in group 3 during the start of the experiment (week 1) and the end (week 8).

Farabaugh *et al* (1994) carried out an experiment with a similar protocol to the present study. They housed budgerigars together that had had no previous experience of one another, and therefore possessed different dominant calls, and traced the development of each bird's call. After only one week, some individuals were matching their cagemates' calls and by the end of the eighth week of the experiment, all birds had the same group specific call.

According to the cross-correlation technique used in this study, budgerigars with no previous experience of one another started to modify their dominant contact calls almost immediately within the first week of being housed together with new flockmates. Judging by the relatively consistent rise in the PCVs (peak correlation values) of comparisons between the calls of pairs, this convergence was rapid and steady in progress and culminated in a new contact call that was shared by all interacting group members.

Farabaugh *et al.* (1994) found that, despite the sharing of a group specific call by all flock members after eight weeks, during the study certain individuals tended to copy parts of others' calls more closely. Though these assessments were based on the visual inspection of sonagrams of the calls, it nevertheless suggests a tendency for certain individuals to match each other more closely, in which case there must be some factors, social or otherwise, influencing the decision of tutor or model choice.

For social rivals, vocal learning is guided by aggressive interactions. Both wild and domesticated male zebra finches usually imitate their fathers (Zann, 1990), and aggression by fathers towards sons may often occur, especially when the next brood hatches.

Clayton (1987) found that young zebra finches, given a choice of two tutors, would tend to learn their song from the one that exhibited most aggression towards them.

Aggressive territorial interactions may often account for shared song; interspecific territorial interactions lead to interspecific vocal mimicry in sparrows (Catchpole & Baptista, 1988). Aggressive interactions can also be related to shared vocalisations in parrots; a tame eclectus parrot (*Eclectus roratus*) mimicked the voice quality and words of a human social rival, and sometimes repeated this imitation immediately prior to aggressive attacks on her rival (Brown & Farabaugh, 1997).

In the present experiment, aggression did not affect the acquisition of new vocalisations to any significant degree. However, this was not perhaps unexpected considering the strong link between preening and proximity, and the apparent negative correlation between these factors and aggression. Indeed there was perhaps a suggestion that aggression appeared to adversely affect call matching, so that members of a group that were observed to be most aggressive to each other, consequently copied each other to a lesser extent. Similarly Casey & Baker (1993) found that in white-crowned sparrows, juveniles showed limited learning of song from adult males that were very aggressive to them. The difference in the present experiment was that learning was between two adults and not a juvenile learning from an adult, as in the studies on zebra finches. Adults are probably less likely to be influenced by aggression in their choice of tutor, considering their relatively higher dominance standing and experience within a flock.

Though it is necessary to be cautious in postulating the results of correlations, since correlation does not necessarily imply causation (Jones & Slater, 1996), it is possible to determine that certain factors are more influencial than others in determining what is learnt and from whom.

In her study, Clayton (1987) also found that other behavioural interactions, such as clumping and preening, had no significant effect on tutor choice, nor did tutor song output. In contrast, the results of this study suggest that the extent of call matching between budgerigars appears to be most related to how much preening a pair indulges

in. Also positively correlated to the extent of call matching was the proximity of a pair. The fact that preening, and to a lesser degree proximity, were related to call matching, suggests that individuals which formed closer social bonds are likely to copy one another more accurately.

If shared sounds are important in intra-group communication, vocal imitation should reflect social interactions. Brown (1985) examined concurrent vocal and social processes in American crows. Individuals with no prior experience of one another, were introduced into an aviary and their behaviours and vocalisations recorded over a three month period. The percentage of aggressive and defensive behaviours (e.g. pecks and agonistic postures) decreased over time, whereas the percentage of affiliative behaviours (e.g. food-sharing and touching) increased, culminating in mutual allopreening. Over the same period, there was progressive imitation of social companions' coo syllables, which were sometimes used exclusively in place of the individual's original call, during social interactions. Brown concluded that vocal imitation was the mechanism that resulted in shared song, and that shared song was related to affiliative interactions and the formation of social bonds.

In this study it is not suggested that if two individuals preen one another more, they will necessarily be predisposed to copy each other's dominant call more accurately. Instead, it is likely that the action of mutual preening is an indication of the pair's close social relationship within the group, and that it is the tendency to match social companions that is the important point.

Affiliative, rather than aggressive, social interactions are clearly associated with learning and the use of shared vocalisations in budgerigars. Other examples of species in which affiliative interactions are associated with vocal learning include African grey parrots (*Psittacus erithacus*) (Pepperberg, 1985, 1994), and European starlings (*Sturnus vulgaris*) (West *et al.*, 1983). Brown-headed cowbirds will change their vocalisations by

trial-and-error learning according to preferences shown by non-vocalising females, based on affiliative interactions (West & King, 1985, 1988).

Other clues to the social relationships within the group are proximity, which showed a modest correlation with call similarity, and aggression, which showed a negative (though not significant) correlation. Though close companions within a wild flock of budgerigars tend to associate more (Brereton, 1963), it is usually only mated pairs that are observed to mutually preen each other. In the absence of females, male budgerigars will form close social bonds with other males in a group, and mutual preening is often seen (pers. observ.). Proximity may be a poor measure of the social bonds, particularly within the confines of a cage, because of the constant movement of individuals that are feeding, drinking and exercising, whereas the action of preening in birds is a highly social and intimate interaction which is only conducted with chosen individuals. In these respects it can be a reliable measure of social bonds.

Tutor song output did not have any significant effect on tutor choice in zebra finches (Clayton, 1987). Similarly calling rate in budgerigars did not influence the tendency for an individual to copy or be copied. There are certain reasons for supposing that birds which call most might be predisposed to be copied more than those with a lesser song output. In budgerigars, as in cardueline finches and chickadees, the learned calls, known as contact calls, are used when the social group or mated pair is in flight, when birds are separated from their social group, and when mates greet one another after separation (Ficken, Ficken & Witkin, 1978; Hailman, Ficken & Ficken, 1985; Mammen & Nowicki, 1981; Mundinger, 1970, 1979; Wyndham, 1980). An individual with a high rate of calling might confer on a copier some social advantage within the flock, such as a greater attractiveness to females, or perhaps simply because a bird calls more and is therefore heard more, it is more likely to be copied by its cagemates. It may be that birds with a high rate of calling are able to practice modifications in their calls to a greater extent than quieter flock members, in which case these birds would be expected

to engage in the most copying. However, a clear effect of calling rate on the extent of matching was not detected in the present experiment.

Clayton's zebra finches did not base their choice of tutor on the dominance of the individuals concerned. However, dominance as such, is a complex quantity to assess in any group size, because it manifests itself in many observable behaviours and is, more often than not, non-linear (Appleby, 1983; Boyd and Silk, 1983). Groups of caged budgerigars form dominance hierarchies (Brereton, 1963), but these hierachies are not stable and may change daily. In addition there is a very high probability that a set of data can be arranged to form a linear dominance hierarchy when none exists in reality (Appleby, 1983). This is especially likely when the sample group is small, as in this experiment. Dominance hierarchies were constructed from a matrix of aggressive interactions which were won and lost, but Landau's index revealed no linearity in the hierarchy. Aggression did not, however, appear to be significantly related to the number of individuals that copied an individual or that a bird copied.

It is perhaps not suprising that the studies on so called 'age-dependent' learners, such as zebra finches by Clayton (1987) and Jones & Slater (1996), reveal differences to the present study, in terms of which factors in a bird's physical and social environment are most influencial in determining the choice of tutor and the extent of learning. Apart from anything else, these studies were dealing with song learning, which has different implications to call learning in the wild.

Song in many passerines, is essentially used in territory defence and mate attraction (Catchpole & Slater, 1995). Calls, and more specifically contact calls, are generally thought to be less prone to seasonal or motivational change (in the zebra finch at least) and tend to function as communicative signals within a flock. Song may therefore tend to be influenced more by factors such as aggression or dominance: learning song from a dominant or aggressive individual may confer a competitive advantage on a tutee. The

learning of calls, on the other hand, may be more affected by social factors such as mutual preening, duetting, feeding and associating in close proximity with other flock members, especially in a highly gregarious and social species such as the budgerigar.

Shared learned vocalisations are thought to function affiliatively within a group in the formation of social bonds (Thorpe, 1961; Thorpe & North, 1965, 1966). In societies of budgerigars (Farabaugh *et al.*, 1994), Australian magpies (Brown & Farabaugh, 1991; Brown & Veltman, 1987; Brown *et al.*, 1988; Farabaugh *et al.*, 1988, 1992b) and American crows (Brown, 1985), long-term associations between mutually well-known individuals are the norm, yet an individual's social environment can change as it moves from one social group to another over the course of its life. In all three species, individuals share vocalisations that are used in affiliative contexts; magpies in the same group exhibit more sharing of the less aggressive warble song, crows share non-territorial song, and budgerigars share contact calls. Vocal learning is related to affiliative social interactions: magpies share most with groupmates and neighbours, crows show increased vocal imitation with increased affiliative and decreased aggressive interactions, and budgerigars preferentially develop shared cells with birds with whom they can interact as flockmates. Both sexes are integral members of the social groups in all three species, and both sexes exhibit vocal sharing. In budgerigars, both sexes exhibit vocal learning of song, and both males and females learn contact calls.

The type of call learning that was observed in this experiment also differed from most studies of song and call learning, in that the subjects used were all mature adults which already possessed a normal repertoire of calls. In these respects, the individuals concerned may be less influenced by factors which juvenile subordinate animals might be more prone to, such as the aggression of an older, more dominant bird. Conducting a similar experiment with juvenile budgerigars might reveal that other factors were more important at a young age.

There are several shortcomings when trying to determine degrees of call matching, and linking this with observations of social behaviours. One problem is in quantifying the extent of copying between pairs in a species in which flock members all share a group specific call, and therefore any differences between pairs are liable to be very subtle. Obviously, this only becomes apparent once individuals have begun to converge in the characteristics of their calls.

Although individuals had been selected for possessing different contact calls, and were completely unfamiliar with one another prior to the commencement of the experiment, there would always be some individuals whose vocalisations were coincidentally more similar to certain group members than others. This imposes a 'head start' as it were, in the development of the individuals call to match that of its cagemates. A pair may therefore have a high PCV after eight weeks, even if the actual amount of change to their calls has been less extensive than in other pairs which have a lower final PCV because their initial PCV was also lower, but the percentage change index did however account for this. It may of course be the case that birds that possessed more similar calls from the onset, did not undergo as great a transformation in their calls during the experiment because they did not need to modify so much to reach the same level of convergence.

The question that arises is which pairs have matched each other more? Is it the pair that has undergone the greatest change in the PCV with much modification of their contact calls? Or is it the pair which were relatively more similar in their calls from the onset and therefore did not need to undergo such changes in their calls to gain a high PCV at the end of the study? The method used was to incorporate both the change in the PCV and the final PCV by quantifying the percentage change in the PCV and this appears to have been satisfactory in determining the relative matching of calls.

Many of the species that have been shown to learn calls form stable social groups for at least part of the year, which makes recognition of, and contact between, particular birds potentially important (Glase, 1973). These large groups are usually quite mobile, and contact calls may aid in the coordination of synchronous group movements, even when the group temporarily joins larger amalgamations of similar groups: for example, black-capped chickadees form large mobile foraging flocks in winter, and these flocks have stable membership (Glase, 1973; Smith, 1984, 1987, 1988).

Shared calls can allow both individual and group recognition. Mammen & Nowicki (1981) found that different flocks of chickadees possessed distinctive group specific calls and also demonstrated that individuals can discriminate their own flockmates' calls from those of other flocks (Nowicki, 1983). Despite the apparent call stereotypy within chickadee flocks, some characteristics of their calls retain individual variability (Nowicki, 1989), and may thus allow individual recognition within the flock. Budgerigars can also easily discriminate call types, and even individual versions of the same shared contact call (Brown *et. al.,* 1988).

There are obvious subtle differences in the shared contact call between budgerigars in a group. Having a group specific contact call, or group 'membership badge' (Treisman, 1978), has apparent advantages in aiding synchronisation and coordination of a flocks movements, yet there also appears to be enough variation on a individual level to allow the recognition of specific birds within the group.

There do not appear to be individuals within a group that are more predisposed to being copied than others. In other words, individuals seem to match others as a consequence of being socially intimate, and not choosing to copy a bird that was particularly appealing as a model for reasons such as aggression or calling rate.

If vocal learning has evolved so that an individual shares vocalisations with a subset of conspecifics with which it interacts on a regular basis, it is perhaps not surprising that social factors affect what, when, and from whom an individual learns. Even in species that do not produce learned vocalisations, social interactions can affect the performance and perception of vocalisations. Gottlieb (1991) demonstrated that ducklings' preference for sounds was affected by the social conditions in which they were reared.

Whether or not budgerigars chose to match more closely the characteristics of their calls with closer social companions, or whether simply being in association for longer with a particular individual allows a pair to copy one another better was unclear. However, this study has reaffirmed the importance of a social context in the learning of new vocalisations and indicated that the presence of close social bonds within a group, inevitably promotes this learning process.

CHAPTER 6

THE AFFECT OF NEW RECRUITS ON THE FLOCK SPECIFIC CALL OF BUDGERIGARS

6.1. Introduction

There have been many studies to investigate the importance of social factors on the learning of song and calls (Baptista & Petrinovich, 1984, 1986; Slater *et. al.*, 1988, Mann, 1991; Jones, 1994).

The importance of a relevant social context on the learning of new calls by budgerigars was examined in chapter 4. Although it was found that budgerigars can learn new calls from non-interactive tape recordings of a conspecific, in most cases learning was very limited or did not occur at all.

In some passerine species, adult birds can acquire songs and calls through mutual imitation of social companions, territorial rivals (Bertram, 1970; Brown, 1985; Brown *et al.,* 1988; Kroodsma, 1974; Margoliash *et al,* 1991; Marler & Mundinger, 1975; McGregor & Krebs, 1982), and heterospecifics (Robinson, 1956). Social factors also appear to be critical for imitation of human speech by birds (Pepperberg & Neapolitan, 1988).

Farabaugh *et al.* (1994) found that if budgerigars with no prior experience of one another, and whose calls were consequently different, were housed together, then after a period of eight weeks all birds had converged in the characteristics of their call so that they all gave the same call type. This provided strong evidence that budgerigars exhibit

considerable vocal plasticity in the learning of new contact calls when their social situation is altered.

Examination of the contact call repertoires on a weekly basis provided evidence that call convergence in budgerigars was achieved through mutual vocal imitation. In the early stages of the experiment however, certain individuals were observed to be acting more as models from which other cagemates would imitate. In addition to imitation of a complete call, they also found frequent recombination of calls, where new calls were formed from part of one of their own call types combined with part of another bird's call type. Once convergence was achieved through imitation and recombination, the structure of the group specific call would continue to change synchronously among all individuals, though they were unable to detect which bird initiated these subtle improvisations of the shared call type. A similar pattern of simultaneous change was found in the shared colony-specific songs of yellow-rumped caciques (*Cacicus cela*; Trainer, 1989).

The addition of new call types can occur within less than a week of contact with new conspecifics. Such rapid modification of calls has also been described for black-capped chickadees (Nowicki, 1989) and European siskins (Mundinger, 1970).

In chapter 5, it was found that certain budgerigars within a captive group were more subtely similar in the characteristics of the group specific call than to others. This may simply be due to the fact that no particular cross-correlations between pairs of individuals are going to give the same peak correlation values, but the similarity between certain individuals did appear to be significantly related to the proportion of time that any particular pair spent together, thus suggesting that social relationships within a group may have influenced the extent of matching.

Neither Farabaugh *et al.* (1994) or Nowicki (1989) could detect whether any single individual appeared to provide a vocal model that other birds copied and they concluded that call convergence occurs through mutual imitation. In both these studies however, none of the individuals used had had any prior experience of one another, in which case it is unlikely that social factors had any initial major influence on the choice of conspecific to imitate. It is conceivable though, that each individual socialised more with those cagemates whose call was most like that of their previous companions.

It could be said that these experiments on captive birds are very artificial, particularly when the results are used to explain possible functions of call convergence in wild populations. Chickadees form large mobile flocks in winter and budgerigars live in flocks outside of the breeding season, but it is unlikely that these huge social groups form suddenly within a very short period of time so that all group members are equally inexperienced with one another. More likely is a situation where new individuals are constantly being recruited into the flock, so that at any particular time the group consists of individuals of varying experience with one another and with correspondingly different levels of call convergence.

The aims of this experiment were therefore to observe the process of call convergence in a captive group of budgerigars that is more akin to a wild flock, by introducing a new recruit into an already established group. The dominant calls of all individuals were traced throughout the experiment to examine whether new birds alter their call to that of the group specific one, or whether all individuals undergo a change in their call. It was hoped that the results would give insight into the functional significance of call convergence in wild populations.

6.2. Methods

Nine adult male budgerigars (*Melopsittacus undulatus*) of varying colour morphs, were selected from a captive aviary flock. The birds had been housed together for at least the previous 12 months. They were each individually recorded in a sound attenuation chamber in order to collect a sample of approximately 100 calls from their repertoire. These recordings were analysed by eye using the Kay DSP Digital Sonagraph and classified into call types based on the structure of the calls. The dominant contact call was categorised as being the call type that is given by an individual on the majority of occasions and in most cases constituted over 80% of the total number of calls given during a recording session. It was striking from observation of the sonagrams of these dominant contact calls that all birds possessed very similar dominant contact calls.

The nine budgerigars were separated into three groups of three birds each, and housed in cages 50 x 150 x 50 cm (see Fig. 5.1). Each group was isolated from all other groups by placing them in separate rooms where they could not interact visually or acoustically with any other conspecifics other than their assigned cagemates. The room was placed on a 14/10 daily light cycle and the birds were fed and provided with fresh water daily. The groups were permitted to settle in their new environment for a period of one week prior to the commencement of the experiment.

Three more adult male budgerigars were obtained from a breeder. They were recorded in the sound attenuation chamber where 100 calls were collected and the dominant contact call was identified as described above. These initial recordings were used at a later date to detect whether the call had changed over the duration of the study.

One bird was then placed in each of the three established budgerigar groups. Prior to this time, the 'new' budgerigar had had no previous experience of any of its cagemates and indeed its dominant call was strikingly different in structure to the flock specific

call of the established group. The day of the addition of the new budgerigar was known as day 1 and from this time all individuals within the flock were recorded every four days for the duration of the 10 week study.

Individuals were removed in turn from the cage and brought to another room to be recorded in the sound attenuation chamber fitted with a Sennheiser MD 400 microphone (frequency response of 1000-10 000 Hz ± 6dB). Each recording session usually lasted no more than 20 minutes, during which a sample of approximately 20-50 calls were collected, but no less than 10. The birds were sometimes played conspecific calls through a Sony SRS-A20 2 Watt speaker fitted inside the sound attenuation chamber in order to initiate a calling response if this was lacking. Other than this occasional brief playback, the budgerigars did not experience any sight or sound of another conspecific within the confines of the room they were housed in or the recording environment. As soon as the required number of calls had been collected, the subject was returned to its group cage and the same process repeated with another bird.

Comparisons of calls between individuals over the ten weeks, were made by cross-correlations of the spectrograms of the digitised recordings along the time axis, using Engineering Design's SIGNAL (version 3.0) software (using a Hanning window; sampling rate of 20 000 Hz; upper frequency limit of 8 kHz; Fast Fourier Transfer (FFT) size of 512; FFT interval of 13.2 sec; frequency resolution of 39.1 Hz; time resolution of 25.6 msec).

6.3. Results

The dominant contact calls of each of the four birds within the three groups were compared by cross-correlations. The peak correlation values (PCV), representing the highest measure of similarity between any two calls being analysed, are shown in Figs.

6.1.1-6.3.6. Calls between all individuals were compared for each four day recording session in order to trace the process of call convergence.

In group 1 it was the budgerigar known as Frank which was the 'new recruit'; in group 2 it was Ren and in group 3 it was Roger. All other birds were members of the 'established flock' which shared the same group specific call. This is reflected in the PCVs of these birds in figs 6.1.4., 6.1.5. and 6.1.6. for group 1; figs 6.2.4., 6.2.5. and 6.2.6. for group 2; and figs 6.3.4., 6.3.5. and 6.3.6. for group 3. Established flock members all had high PCVs of between 0.8 to 0.96 which were indicative of very similar calls. New recruits at day 1 had PCVs with their stranger cagemates of between 0.6 and 0.75, showing very little similarity in their calls with the group specific call.

In figures 6.1.1-6.1.3, 6.2.1-6.2.3, and 6.3.1-6.3.3 it is evident from the increasing PCVs, that the calls of new recruits undergo a gradual change so that they become more similar to the calls of their established flock members. In many of the figures, e.g. figs. 6.1.1., 6.1.2., 6.2.1., and 6.2.3., there appears to be a point between recording sessions, when a larger increase in similarity occurred. This period of maximum imitation occurred around the third or fourth week; in group 1, Frank showed the greatest change in his contact call between 20 and 30 days (comparisons vary slightly between each of its cagemates), whereas in group 2, Ren showed the largest increase in PCV prior to 20 days. In group 3, Roger generally showed less imitation than its counterparts in groups 1 and 2, attaining lower PCVs with its cagemates by the end of the 8 weeks, and its period of rapid imitation was less marked than in the other groups at just prior to 20 days.

The mean PCV results between new recruits and their established flock members at the start and end of the experiment, are shown in fig. 6.4. The mean PCVs between each new recruit and its three cagemates at day 1 and day 53 are shown. This figure highlights the trends of figures 6.1.-6.3. in showing that new recruits' dominant contact

Fig.6.1.1. Frank & Joe

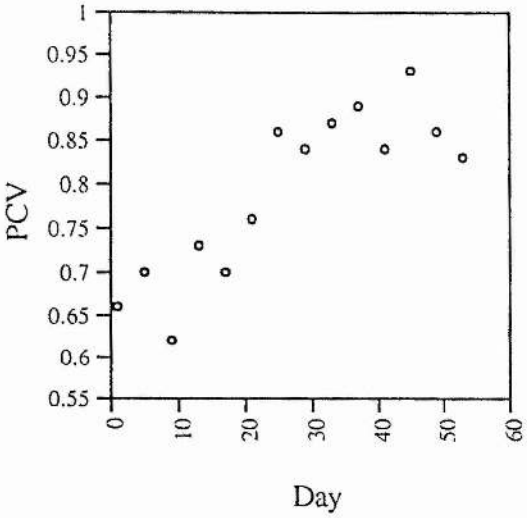


Fig.6.1.2. Frank & Dan

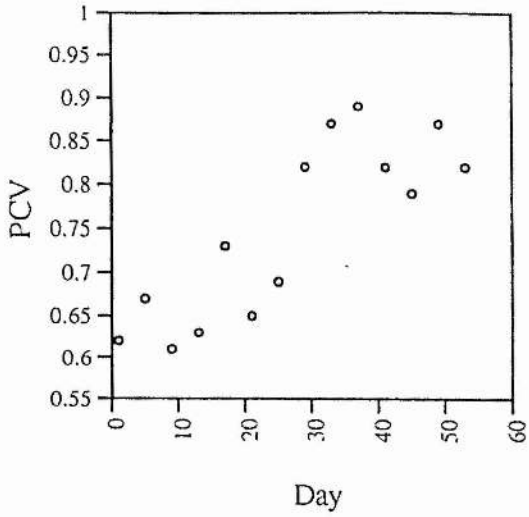


Fig.6.1.3. Frank & Emery

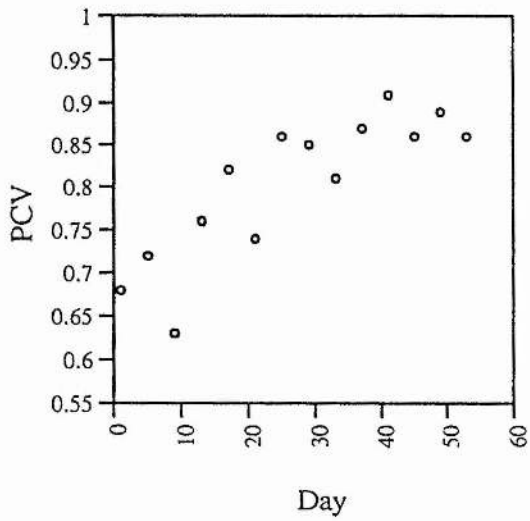


Fig. 6.1.4. Joe & Dan

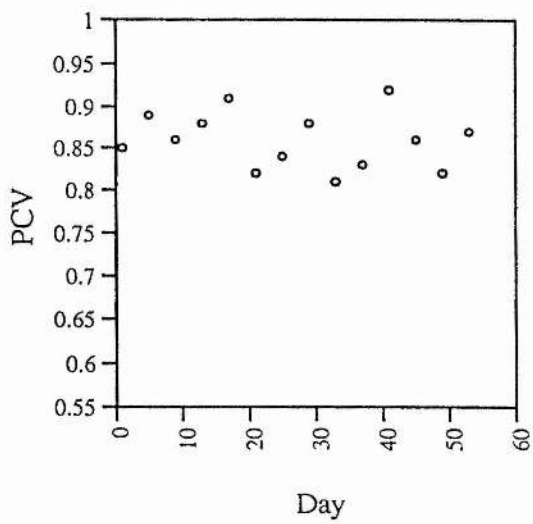


Fig.6.1.5. Joe & Emery

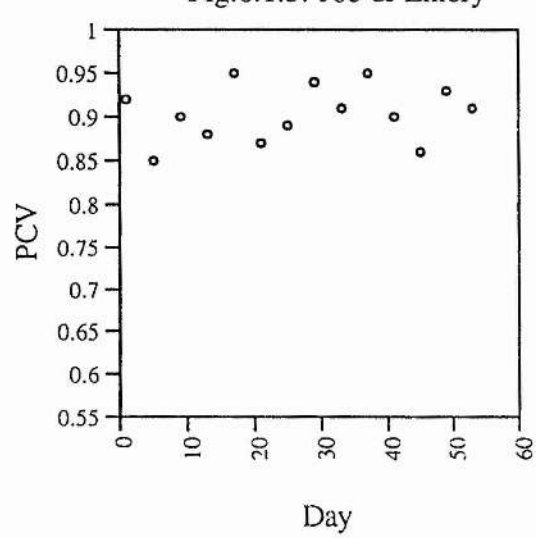


Fig.6.1.6. Dan & Emery

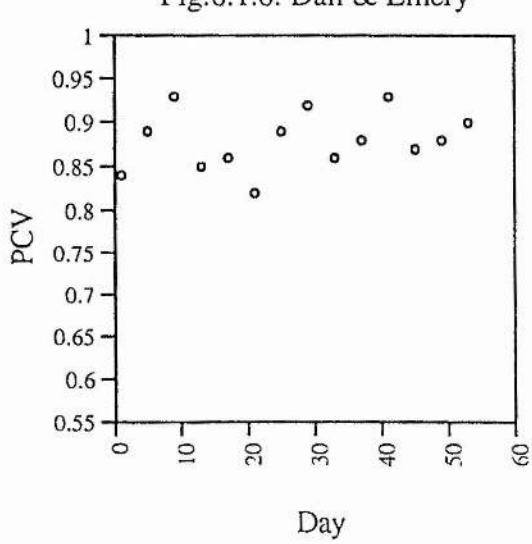


Fig. 6.1.1-6.1.6 Mean peak correlation values (PCV) from cross-correlations of sonagrams of the contact calls between individual budgerigars in group 1 over the duration of the experiment.

Fig.6.2.1. Ren & Matt

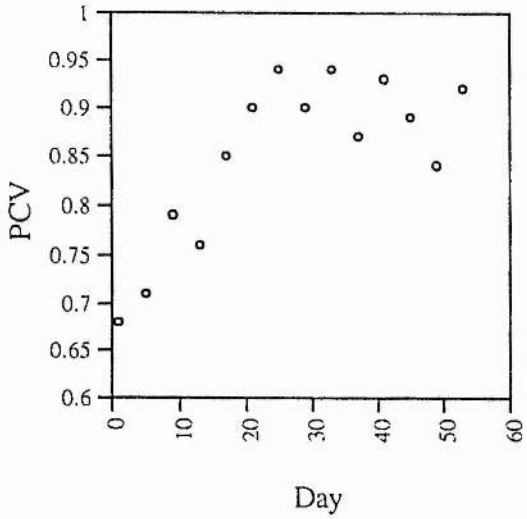


Fig.6.2.2. Ren & Alf

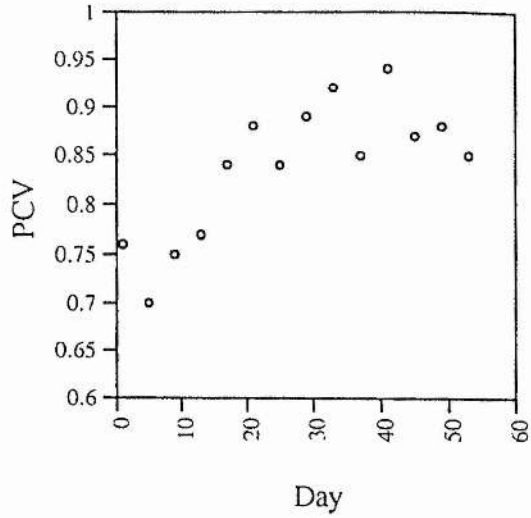


Fig.6.2.3. Ren & Will

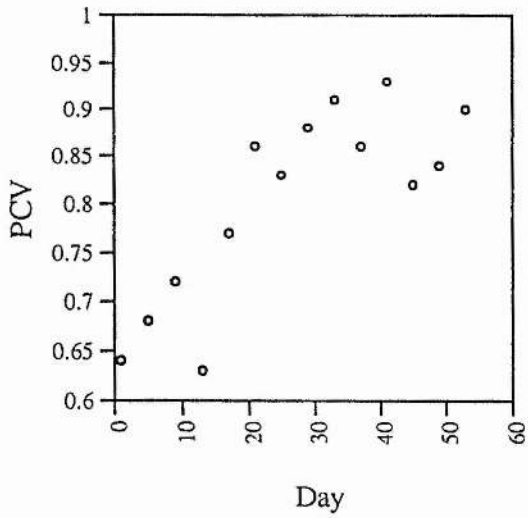


Fig.6.2.4. Matt & Alf

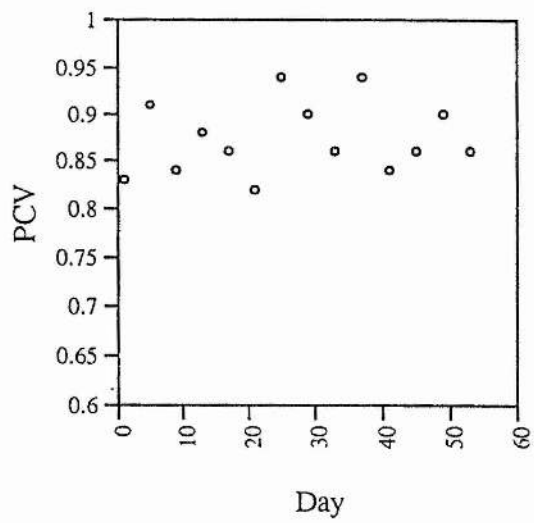


Fig.6.2.5. Matt & Will

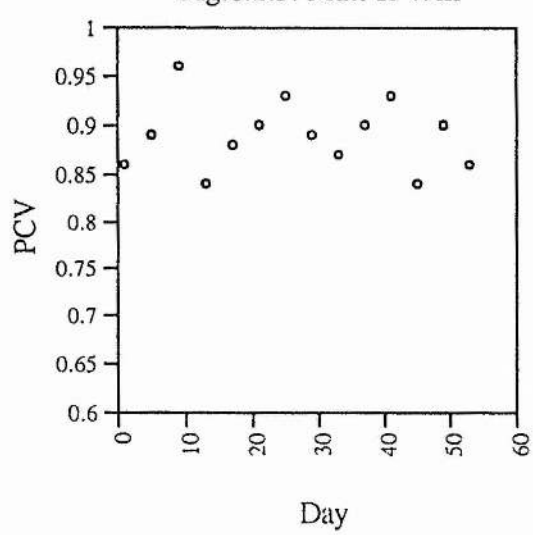


Fig.6.2.6. Alf & Will

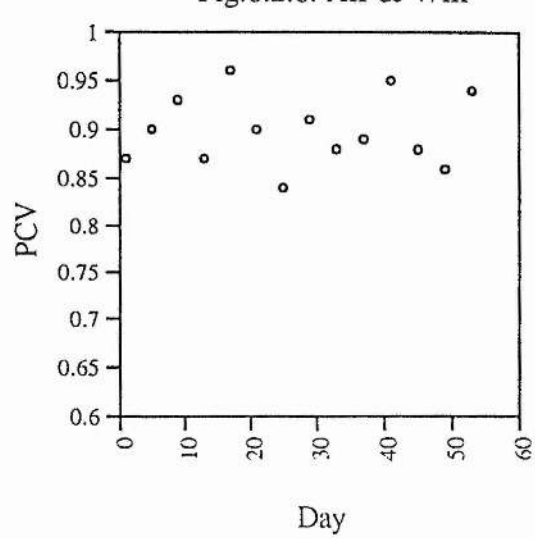


Fig. 6.2.1-6.2.6 Mean peak correlation values (PCV) from cross-correlations of sonagrams of the contact calls between individual budgerigars in group 2 over the duration of the experiment.

Fig.6.3.1. Roger & Stu

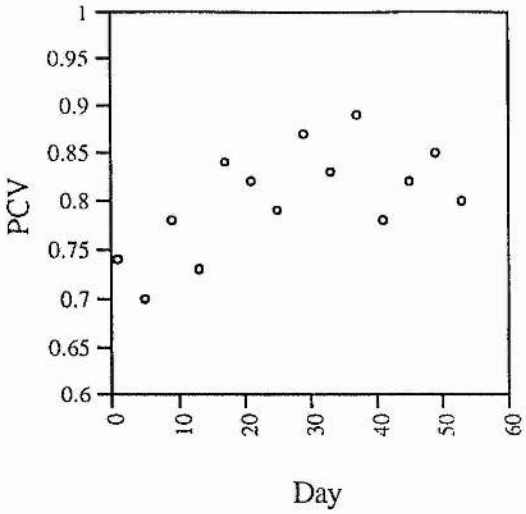


Fig.6.3.2. Roger & Neon

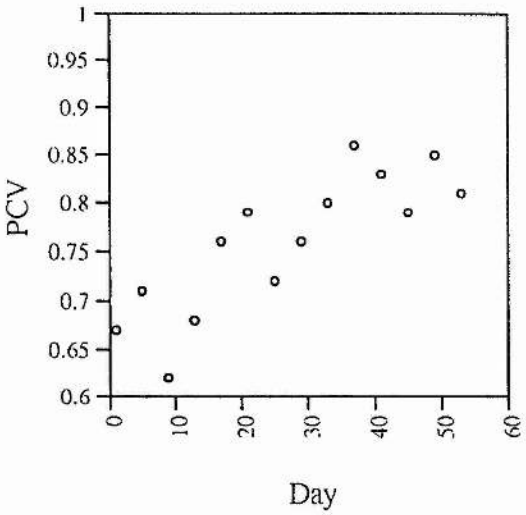


Fig.6.3.3. Roger & Vinny

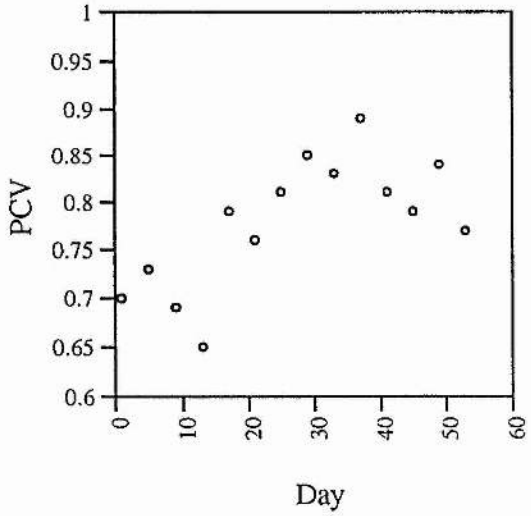


Fig.6.3.4. Stu & Vinny

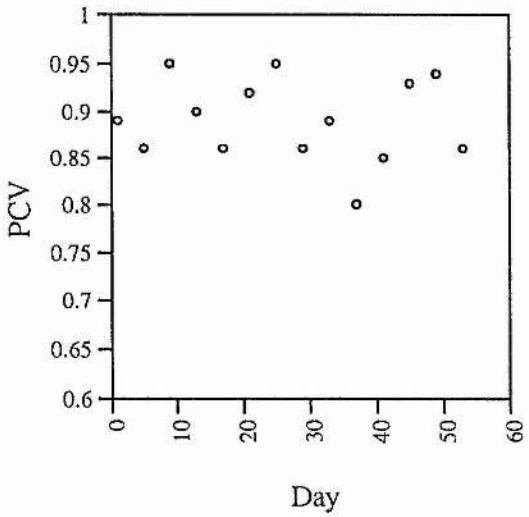


Fig.6.3.5. Stu & Neon

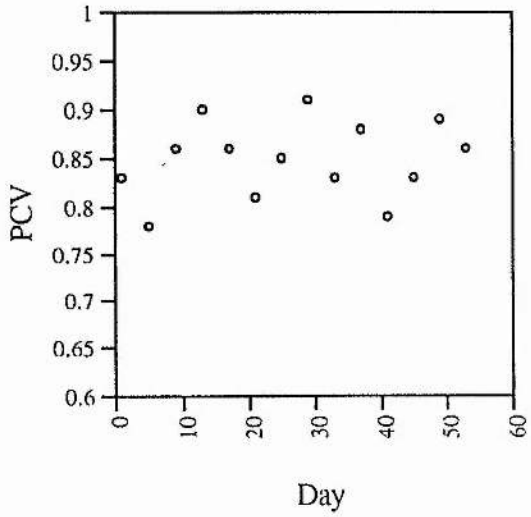


Fig.6.3.6. Neon & Vinny

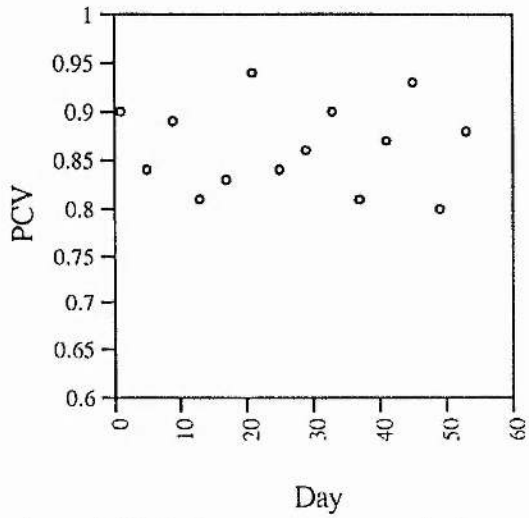


Fig. 6.3.1-6.3.6 Mean peak correlation values (PCV) from cross-correlations of sonagrams of the contact calls between individual budgerigars in group 3 over the duration of the experiment.

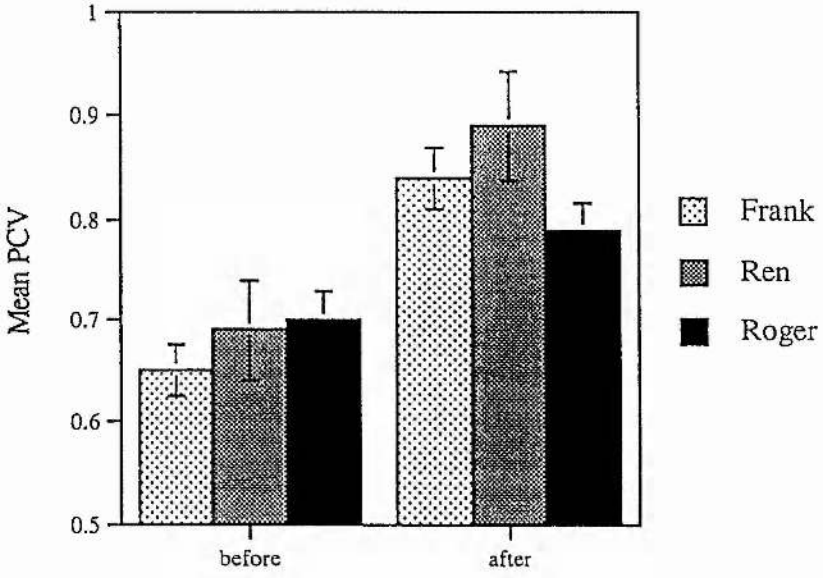


Fig. 6.4 The mean peak correlation values (PCV) from cross correlations of calls between new recruits and established flock members at the start and end of the study. Individuals marked are new recruits from each of the three groups. Standard deviation bars are shown.

calls were more similar to established flock members after the eight week period than at the start. This was confirmed by bootstrapping the results at the start of the experiment with those at the end: for Frank in group 1 ($z = 4.10$, $P<0.01$); for Ren in group 2 ($z = 3.81$, $P<0.01$); Roger in group 3 ($z = 3.15$, $P<0.01$).

Table 6.1. shows the z-score results from 500 bootstrap comparisons of the PCVs between members of each group. Comparisons were made between the PCVs of each pair at the start of the experiment with the end of the experiment. For instance, Frank and Joe's mean PCV (from cross-correlation of their contact calls) at the start of the study was compared by bootstrapping with Frank and Joe's mean PCV at the end of the eight weeks. This was repeated for every pair comparison in each of the three groups.

From Table 6.1. it can be seen that the only difference in the PCV with time occurred in comparisons between the calls of established flock members and the new recruits. There was no significant change in the PCVs between established flock members over the duration of the experiment, meaning that their calls were equally similar for the eight weeks. This indicates that there was a significant increase in similarity of new recruits and their cagemates, and suggests that this was entirely due to the new birds converging on the group specific call of the established groups, rather than the group converging on the new recruit or mutual convergence of all subjects.

Further evidence to suggest it was the new recruits that were conforming to the group's call is found in figures 6.5.1-6.5.4, 6.6.1-6.6.4, and 6.7.1-6.7.4. These figures illustrate how the call changes on an individual level, over the duration of the experiment, by showing the PCVs from cross-correlations between recordings of the call at each four day interval, with a sample of the bird's call on day 1. It is therefore an indication of how much the call is changing over time, compared to how it was before.

Bootstrap comparison	z-score	Significance level
Frank & Joe	3.11	**P<0.01**
Frank & Dan	3.32	**P<0.01**
Frank & Emery	2.98	**P<0.01**
Joe & Dan	0.95	P>0.05
Joe & Emery	0.42	P>0.05
Dan & Emery	0.78	P>0.05
Ren & Matt	2.71	**P<0.01**
Ren & Alf	2.52	**P<0.05**
Ren & Will	2.98	**P<0.01**
Matt & Alf	1.19	P>0.05
Matt & Will	0.95	P>0.05
Alf & Will	1.70	P>0.05
Roger & Stu	2.40	**P<0.05**
Roger & Neon	2.85	**P<0.01**
Roger & Vinny	2.29	**P<0.05**
Stu & Neon	0.60	P>0.05
Stu & Vinny	0.53	P>0.05
Neon & Vinny	0.86	P>0.05

Table 6.1 Z-score results from 500 bootstrap comparisons between the peak correlation values (PCV) of pairs of individuals at the start and end of the experiment. PCVs were obtained from cross correlations of sonagrams of the calls of two individuals to compare their similarity. The bootstrap analysis between the start and end of the experiment was used to test whether there was a significant change in the similarity of calls between individuals. Any z-scores equal to or above 1.96 (P=0.05) or 2.58 (P=0.01) indicate a significant difference between the two data sets being compared, in this case indicating a significant change in the degree of similarity of calls. For clarification, any values that were significant are in bold type.

Fig.6.5.1. Frank

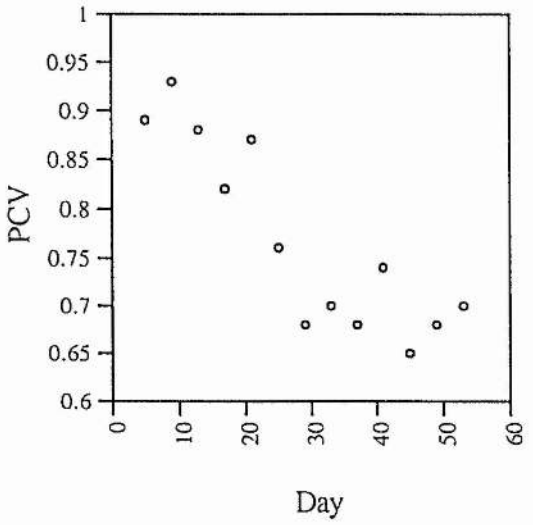


Fig.6.5.2. Joe

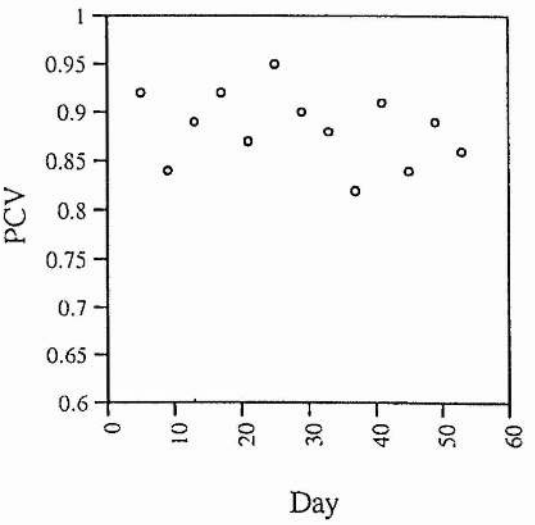


Fig.6.5.3. Dan

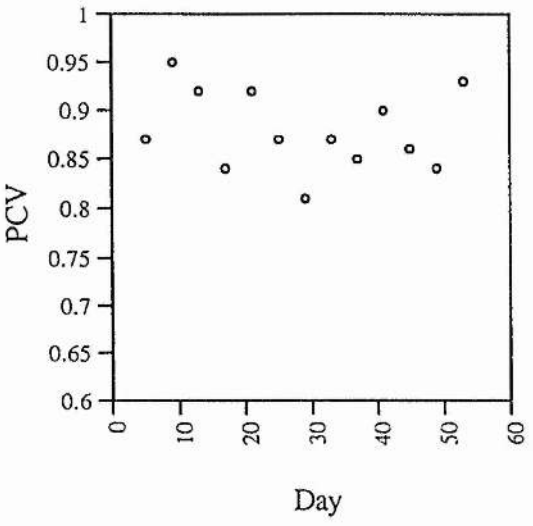
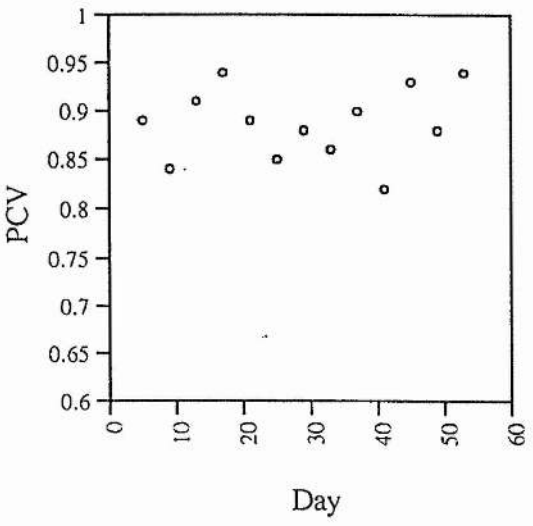


Fig.6.5.4. Emery



Figs. 6.5.1-6.5.4 Peak correlation values (PCV) from cross correlations between recordings of an individual budgerigar's call at each 4 day interval with an initial recording of the call before commencement of the experiment for each bird in group 1. The graphs therefore trace the change in the contact call of each bird over the 8 weeks of the study.

Fig.6.6.1.Ren

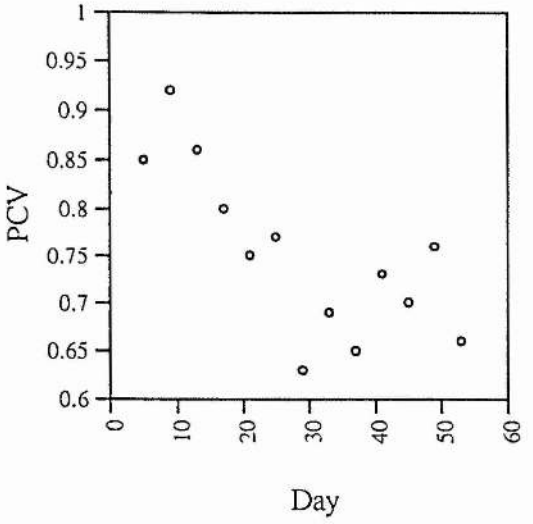


Fig.6.6.2. Matt

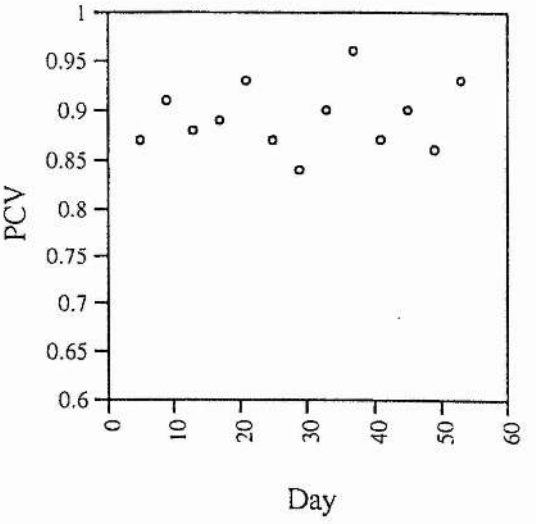


Fig.6.6.3. Alf

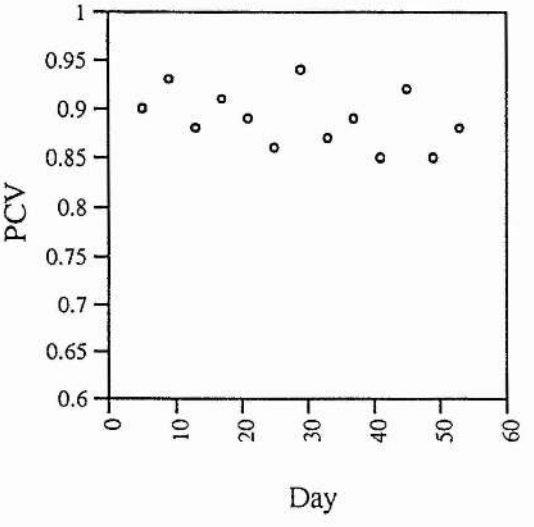
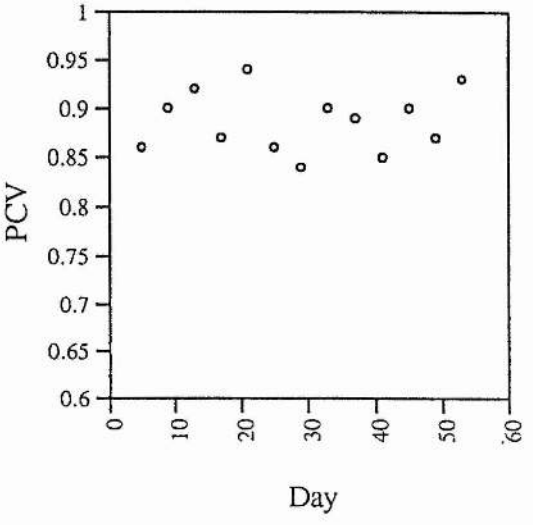


Fig.6.6.4. Will



Figs. 6.6.1-6.6.4 Peak correlation values (PCV) from cross correlations between recordings of an individual budgerigar's call at each 4 day interval with an initial recording of the call before commencement of the experiment for each bird in group 2. The graphs therefore trace the change in the contact call of each bird over the 8 weeks of the study.

Fig.6.7.1.Roger

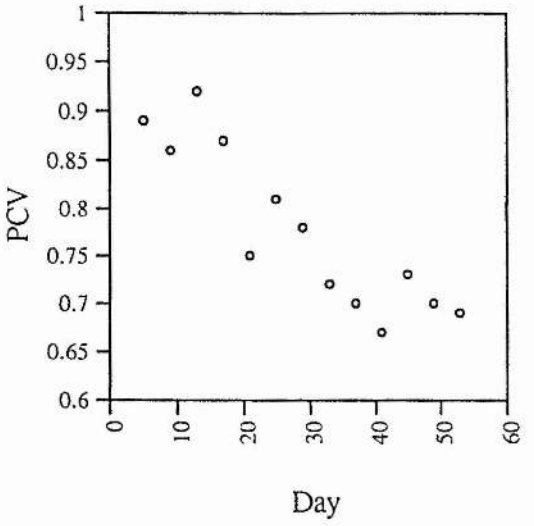


Fig.6.7.2. Stu

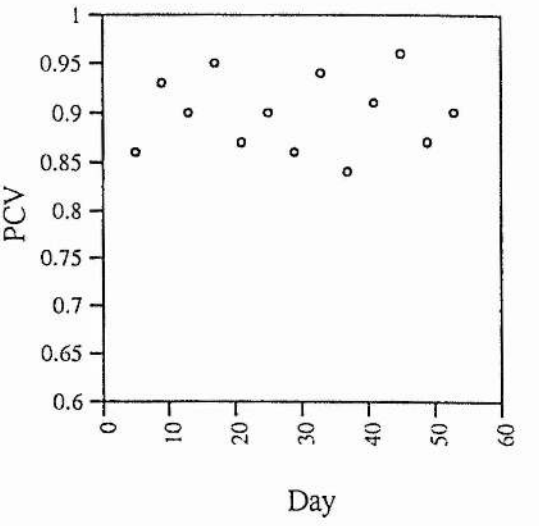


Fig.6.7.3. Neon

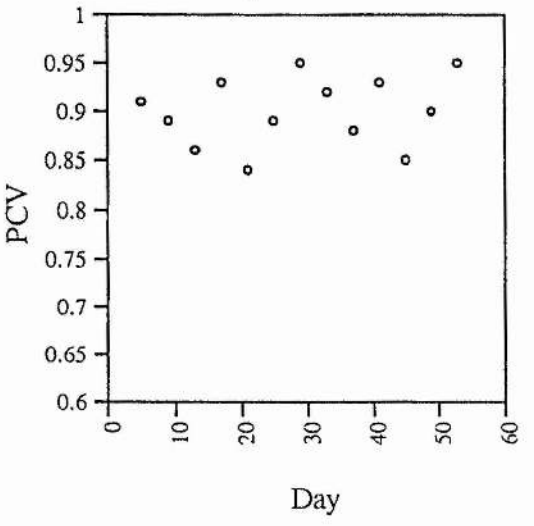
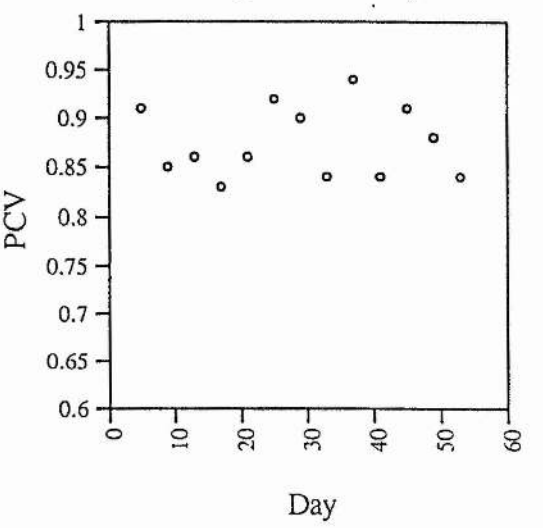


Fig.6.7.4. Vinny



Figs. 6.7.1-6.7.4 Peak correlation values (PCV) from cross correlations between recordings of an individual budgerigar's call at each 4 day interval with an initial recording of the call before commencement of the experiment for each bird in group 3. The graphs therefore trace the change in the contact call of each bird over the 8 weeks of the study.

Referring to figs 6.5.1, 6.6.1 and 6.7.1, all new recruits show a marked and dramatic change in their call; in other words, a divergence in the characteristics of their contact calls. In contrast, established group members show no tendencies to diverge or converge on their initial contact call over the period of eight weeks, despite fluctuations in the PCV of around ± 0.05.

The divergence in the calls of new recruits from the initial call type, appeared to occur at a relatively steady rate. Initially, within the first week, the call has not changed significantly, and the PCVs between successive recordings and the initial sample call show a similarity of around 0.85-0.95 (a figure which indicates that the calls are very similar). Thereafter, in the second week, the call undergoes a change (from figs 6.1.-6.3. we know that this is a convergence on the new groups call) until at about 30 days or so, most alteration to the call is complete.

The change in the contact call for each individual was tested statistically for significance. A total of 500 bootstrap comparisons were carried out between the PCVs of the calls at the start a sample of the call recorded prior to the experiment, and those of the calls at the end with this prior sample. Table 6.2. shows the z-score results from comparisons for each individual. It can be seen that all new recruits (i.e. Frank, Ren and Roger) underwent a significant change in their dominant contact calls. Established group members did not show any significant alteration of their call, except Neon (fig.6.7.3.) whose last recordings appeared to be curiously more similar to the initial call sample than the recordings at the start.

Sonagrams of the dominant calls of all individuals in the three groups at the start and end of the study are shown in Figs. 6.8-6.10. It is clear from these sonagrams, that all established flock members in week 1, had a shared group specific call which differed markedly from the call of new recruits. However, by the eighth week, all cagemates

Bootstrap comparison	z-score	Significance level
Frank	**3.05**	**P<0.01**
Joe	0.96	P>0.05
Dan	1.12	P>0.05
Emery	0.62	P>0.05
Ren	**4.85**	**P<0.01**
Matt	0.84	P>0.05
Alf	0.16	P>0.05
Will	1.77	P>0.05
Roger	**3.38**	**P<0.01**
Stu	0.60	P>0.05
Neon	**2.46**	**P<0.05**
Vinny	0.42	P>0.05

Table 6.2. Z-score results from 500 bootstrap comparisons to test whether there was a significant change in the contact calls of individuals in all three groups. Cross correlations were carried out between successive recordings of the contact call from each individual and compared with a sample of the call recorded prior to the experiment. The resulting peak correlation values (PCV) between the initial recording and the call at the start, and the initial recording and the call at the end were then compared by bootstrapping with the resulting z-scores shown above. Any values equal to or above 1.96 (P=0.05) or 2.58 (P=0.01) indicate a significant change in an individual's call over the duration of the study. Significant scores have been highlighted for clarity in bold type.

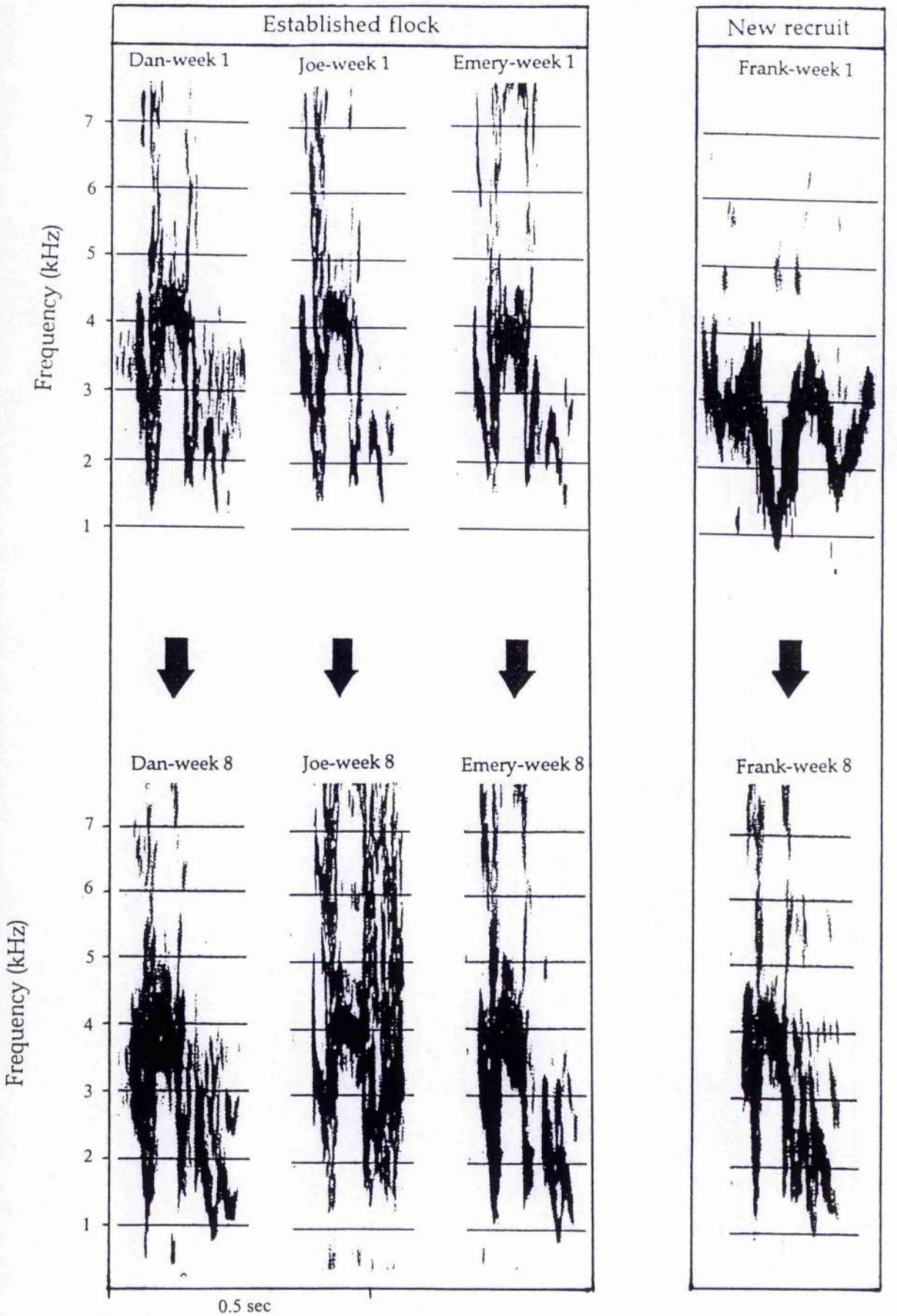


Fig. 6.8 Sonagrams of the calls of individuals in group 1 during the start and end of the study (week 1 and week 8 respectively). The new recruit is shown on the far right.

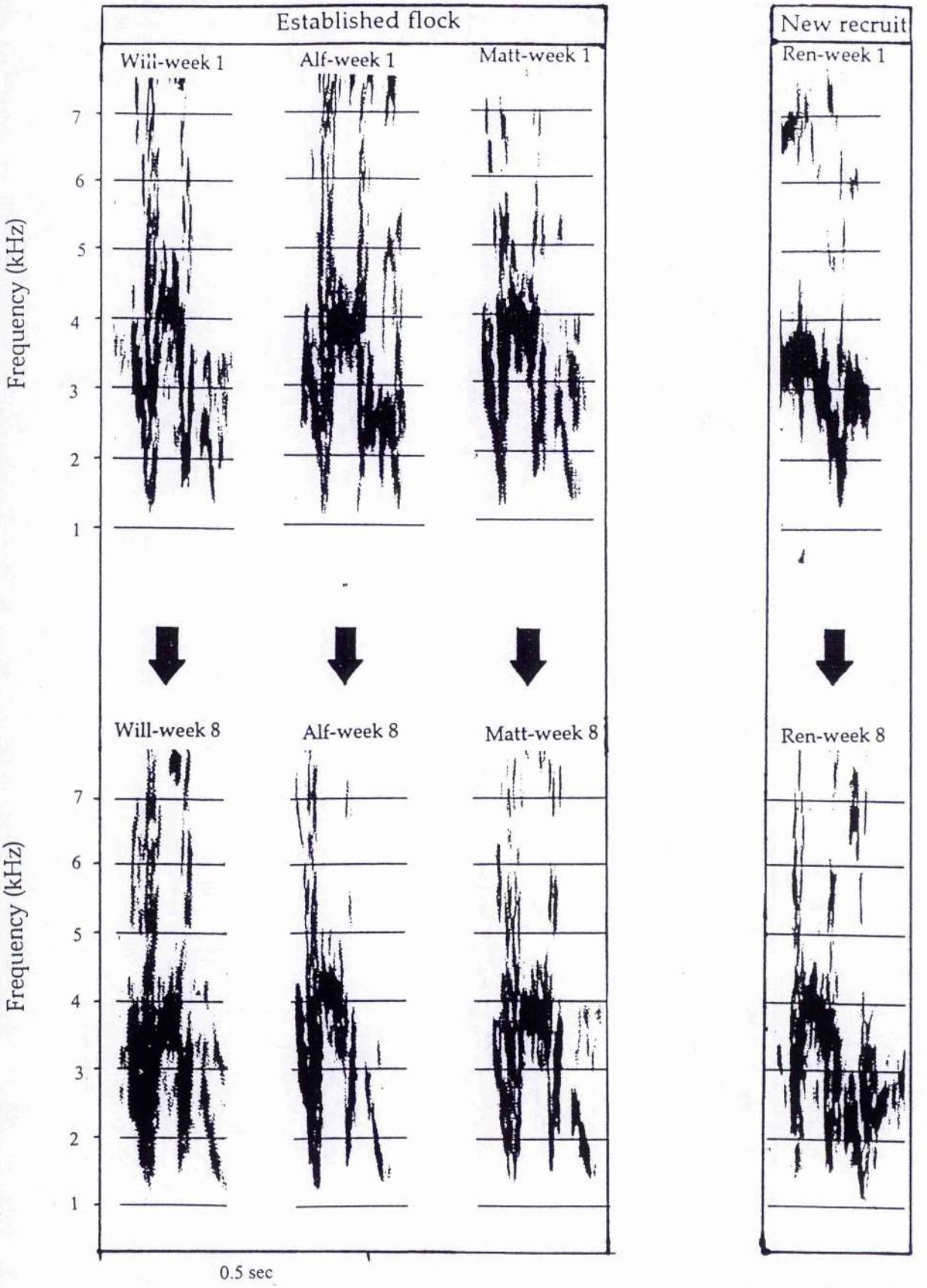


Fig. 6.9 Sonagrams of the calls of individuals in group 2 during the start and end of the study (week 1 and week 8 respectively). The new recruit is shown on the far right.

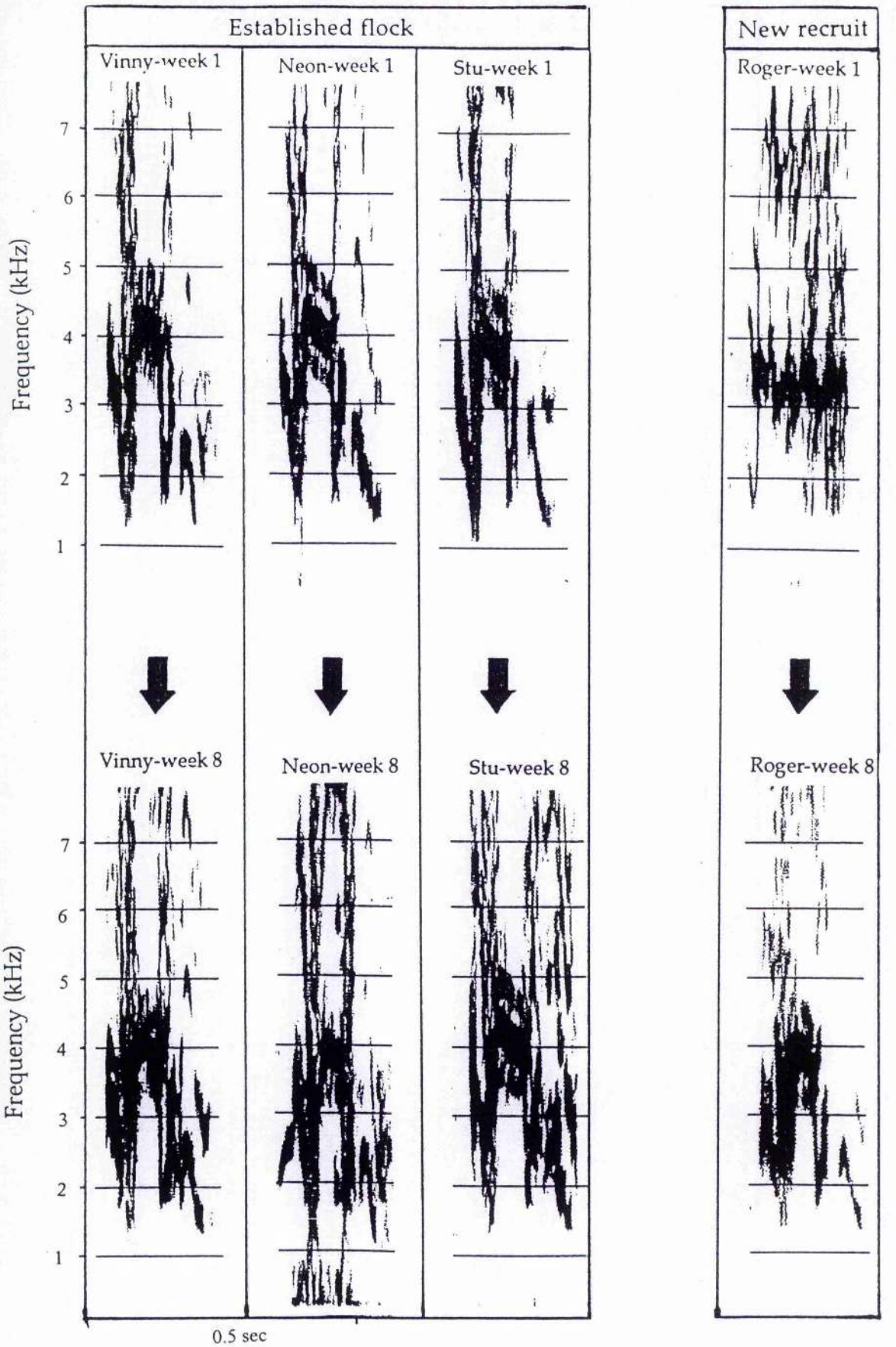


Fig. 6.10 Sonagrams of the calls of individuals in group 3 during the start and end of the study (week 1 and week 8 respectively). The new recruit is shown on the far right.

shared an identical group call, and there was no apparent difference in the pattern of frequency modulation between new recruits and established flock members.

The group specific call of established flock members, does appear to have changed slightly between week 1 and week 8, though cross-correlation analysis did not reveal any significant change. It is known that budgerigar flocks undergo synchronous changes in the group specific call, and this may be what is observed here.

6.4. Discussion

The process of vocal imitation, or more specifically call convergence, has been investigated in several species in some detail: for example, bou-bou shrikes (*Laniarius aethiopicus major*) (Thorpe & North, 1966); American goldfinches (*Carduelis tristis*) (Mundinger, 1970); black-capped chickadees (*Parus atricapillus*) (Mammen & Nowicki, 1981; Nowicki, 1989); budgerigars (*Melopsittacus undulatus*) (Farabaugh *et al.,* 1994). Although not all of these species can be termed as being strictly age independent (i.e. possessing the ability to learn new vocalisations in adulthood), they can all learn new vocalisations within their first year (e.g. many passerine species can learn in their first year, but not at three or four years of age).

The results of some of these studies have been discussed in earlier chapters, but essentially individuals were observed to imitate, with high accuracy, the vocalisations of their conspecific group members. In the case of mated pairs, a benefit of mutual imitation may be that it aids the formation of a pair bond and may assist in individual recognition (Thorpe & North, 1966). However, when imitation *en masse* is observed between apparently unrelated individuals and of both sexes within a social group, the reasons for call convergence become less clear and more speculative.

In chapter 5, budgerigars were found to imitate more accurately from those individuals with whom they associated most, suggesting that social bonds were fairly influencial in the process of call convergence. This is not to claim that birds would only copy those conspecifics which they were closest to (on a social level). Indeed, the results of chapter 4 illustrate clearly that the extent of vocal imitation is probably as much to do with individual capabilities and motivation as it is to do with environmental factors or relationships with others; some budgerigars were able to copy from tapes with a reasonable degree of accuracy, while others showed no such tendencies.

Alternatively, the lack of learning in some individuals, could be as much to do with the limitations of the playback features, rather than individual motivation. Only one call was used in the playback to control for the possible influences of different calls on motivational states, and this effectively limited the experiment to a sample size of n=1.

In order to gain an insight into the possible reasons for many conspecifics to share a group specific call, it is necessary to look more closely at the process of call convergence as it occurs, and observe the development of each individual's call in relation to each of its other group members.

Secondly, it is essential to try and simulate the experimental situation to that of the wild as closely as possible. In, for example, Nowicki's study on black-capped chickadees (1989), five individuals were caught from different wild populations and then housed together to observe call convergence in operation. The vocal behaviour of each individual was then monitored for several weeks. The acoustic analyses revealed that significant vocal convergence occurred in less than one week, and that no single individual appeared to provide the vocal model that other birds copied.

Farabaugh's experiments on budgerigars followed a similar protocol and revealed similar results. None of her subjects had had previous experience with one another prior

to the experiment, and no single individual appeared to be copied more than others. This raises the question of what makes birds that are effectively complete strangers, copy one another ?

As previously mentioned, social relationships within a group appear to be important in deciding who is copied, but this alone cannot account for the imitation of conspecifics.

In criticism of the studies of Nowicki and of Farabaugh, it is perhaps not suprising that mutual imitation was observed, considering all individuals were strangers to each other. In such a situation, there were initially no close social companions, and all individuals were essentially new recruits. This is unlikely to be the case in a wild population, where membership is far from stable due to the movement of birds to and from the flock (Brereton, 1963), but where, at any one point in time, there are likely to be many individuals that are familiar with one another, and which consequently share a common call. The protocol for the present experiment had accounted for this in its design.

In this experiment, a 'new recruit' was added to an 'established flock', which consisted of three birds that were very familiar with one another and which shared a common dominant contact call. It was thought that this would be more representative of a natural situation where a new bird joins a flock in which most individuals share the same call type.

The results of this experiment demonstrate clearly that it is new flock members that alter their dominant contact calls to conform to the group specific call. This was evident from analysing the overall change in the call by cross-correlating subsequent samples of the call recorded every four days with an original sample of the call from day 1. The change in the call is marked by the dramatic decrease in the PCV in new recruits, but a comparatively stable PCV for established group members (the discrepancy for the individual known as Neon, in which its final call type was more similar to the initial at

the end than at the start, is probably the result of poor quality recording affecting the cross-correlation).

Cross-correlations between new recruits and established group members showed clearly that the new birds had imitated well the group specific call of its cagemates. Despite a continuous synchronous change in the dominant contact call by members of a social flock, as described by Farabaugh *et al.* (1994), it was the new recruit in each of the three experimental groups that changed its call to match the members of its new group, and not *vice versa*.

This result differs from the findings of Nowicki (1989) and more appropriately Farabaugh *et al.* (1994), in that it identifies certain individuals (i.e. new group members) as undergoing call convergence, rather than the mutual imitation that was described in these previous studies. Farabaugh did however, initially observe imitation of one bird's original dominant call type by another bird, but later reported that imitation was mutual, with no specific individuals emerging as models and others as imitators.

The obvious explanation for the discrepancy in results between the present study and Farabaugh *et al.*'s, would appear to be the social status of the birds involved. Previous studies have already showed how social factors are highly influencial in determining from whom and what is learnt (Mammen & Nowicki, 1981; Marler & Mundinger, 1975; Mundinger, 1970, 1979; Nowicki, 1989), and indeed the results of chapter 5 indicated that differences in social bonds between group members can affect the extent of imitation between them.

The results of Farabaugh *et al.* and the present experiment are not contradictory, and do in fact tend to support possible functions for call convergence in social species of birds. That new flock members will copy the group specific call, suggests that this perculiar conformity might serve as some sort of mechanism of integration of new members into

a social group (Brown, 1985; Feekes, 1977, 1982; Mundinger, 1970; Thorpe & North, 1965, 1966), and can be used both as passwords, and proclamations of group membership (Feekes, 1977, 1982; Treisman, 1978).

The group specific song of the Australian magpie functions in territorial advertisement and defence, and in intra-group cohesion and communication. Magpie song expresses individual identity, group identity, sex, and the number of group members. Full communal songs are heard most during advertisement and lengthy battles at territorial boundaries, when all groupmates join in highly synchronised co-operative defence. In these contexts, the song probably functions as an aggressive proclamation directed at rivals and also as a rallying cry to incite and co-ordinate groupmates (Brown & Veltman, 1987; Brown & Farabaugh, 1991; Farabaugh *et al.*, 1992b). In non-territorial contexts, group membership is delineated by participation in the communal vocal display (E.D. Brown *et al.*, 1988).

Yellow-rumped caciques breed in colonies, and all individuals within the colony share a repertoire of songs which they use in competition with one another for mates (Trainer, 1987, 1988). However, intruding males that do not possess the colony-specific call can be easily identified, and individuals within the colony collaborate in chasing away competitors (Feekes, 1977, 1982).

There are a number of species from diverse taxa which live in stable social groups for all, or part of the year, and which have a functionally similar learned call that is specific to that group (Mundinger, 1970. 1979; Mammen & Nowicki, 1981; Nowicki, 1983, 1989; Elowson & Snowdon, 1994). Some mammals even imitate the vocalisations of their social companions (e.g. bottlenosed dolphins, *Tursiops truncatus*, Tyack , 1986).

Group-specific contact calls may aid in the co-ordination of synchronous group movement when the group or flock temporarily joins other flocks. Learned shared

contact calls allow group as well as individual recognition for members of the group; budgerigars can easily discriminate among different contact call types, and also between different birds' versions of the shared contact call type (Brown *et al.*, 1988a).

Shared vocalisations may confer certain advantages to individuals; a songbird may gain in assessing the distance of a territorial rival by the degradation of its shared song (Richards, 1981; McGregor & Krebs, 1984), whereas a group-living bird may gain a perceptual advantage in the individual recognition of its groupmates by means of a shared contact call.

The subjects of Farabaugh *et al.*'s study were not presented with a new group in which all birds were familiar with a clear group specific call from which they could imitate. In short, all individuals were as new and unfamiliar as each other, with the result that there appeared to be no clear rules that governed who copied from whom. New calls appeared to be composed of part of one of an individual's own call type combined with part of another bird's call type, so that the process by which birds obtained a shared dominant contact call type was probably a combination of mutual imitation, recombination, and improvisation.

In the present experiment, new birds were introduced into a group of familiar birds that would be indulging in social behaviours such as preening and vocal duetting, and which all possessed the same contact call. This could present a new recruit with a conspicuous model and some motivation to be accepted into the social group. New birds are often the target of aggression by members of a group (pers observations), and therefore the advantages of not being 'the odd one out' are obvious.

Whether imitation of a conspecific's call is more likely to lead to a stable social bond, or whether imitation is a consequence of forming a social bond is still unclear. The present experiment examined whether certain individuals did copy others, and if so, whom. It

did not set out to consider the complexities of behavioural interactions because of the obvious complications of assessing these behaviours (see Chapter 5), and thus the social standing of the group at any particular time was not assessed. It would be interesting to repeat the experiment while determining social interactions simultaneously in order to inter-relate the findings of Chapters 5 and 6. What is evident, is that the process of call convergence is, in itself, liable to be affected by social factors, and that the direction it takes is dependent on the social standings of the individuals involved.

CHAPTER 7

CONCLUSIONS

This thesis has described the results of some experiments which investigated the process of call convergence in an age-independent learner, the budgerigar, and an age-dependent learner, the zebra finch. Chapters 3, 4, 5 and 6 investigated the importance of various social factors in the learning of new vocalisations in adulthood, and the effect that deprivation of these social stimuli had on the ability of these species to learn calls. Chapter 2 returned to the topic of the study of Zann (1985), by investigating similarities in the distance calls (DCs) of zebra finches of varying relatedness to ascertain whether calls were predominantly learned or inherited.

There have been many studies which have highlighted the importance of social factors in vocal learning and how more information can be acquired with a social context (Baptista & Petrinovich, 1984, 1986; Clayton, 1988; Farabaugh *et al.*, 1994; Immelmann, 1969; Jones, 1994; Mann, 1991; Pepperberg, 1990; Slater *et al.*, 1988). Dooling, who reared budgerigars in isolation (1987a) and also deafened nestlings (1987b), found that these birds produced abnormal calls which did not resemble highly frequency modulated calls of normal adults.

Learning in budgerigars is not, by contrast to zebra finches, restricted to a sensitive phase early in development, as demonstrated in Chapters 5 and 6. Brown, Dooling and O'Grady (1988) reported that, if unfamiliar budgerigars were kept together in the same cage, their calls would converge to a group specific call, which was distinct from the common calls of other groups housed separately in the same room. Farabaugh *et al.* (1994) also observed this process of call convergence. In these studies it appeared that close proximity with social companions was a main factor in the vocal plasticity

exhibited by their subjects and that, in the absence of social, but not aural contact, vocal imitation was greatly reduced.

Whether or not social factors are vital for vocal learning to occur was the subject of investigation in Chapter 4. The results appeared to reflect those of Brown, Dooling and O'Grady (1988) in that budgerigars that were placed in acoustic isolation, and only provided with a taped playback of a conspecific on which to model their call, showed very limited learning; only one bird copied the model with any degree of accuracy, and most birds showed little, if nay evidence of call convergence to the tape recording.

There have been studies that have successfully demonstrated learning from tapes. Young swamp sparrows will learn accurately from playbacks of conspecific songs with a complete lack of any social stimuli (Marler & Peters, 1982), nut only if presented during the sensitive phase of learning, when the bird is most attentive. On the other hand, zebra finches appear to need social interaction to learn song (Immelmann, 1969). Young male zebra finches do not passively copy songs that are played to them through loudspeakers (Eales, 1989).

The lack of learning from tapes that was observed in these experiments and in Chapter 4, may be the result of a deficient interactive context. Adret (1993) demonstrated that young zebra finches could learn from tapes if operant conditioning techniques were employed. In his experiments, young zebra finches were required to peck a key for a song 'reward'. It appears that the interaction between the bird pecking a key and the Skinner box 'responding' with conspecific song provided an adequately salient substitute for a live social stimuli.

Pepperberg (1988, 1990) also stresses the importance of an interactive element in vocal learning, and suggests that this can usually only be achieved with a live tutor. Indeed, an interactive tutor can be such a salient stimulus to a subject that non-conspecific

vocalisations and sounds can be imitated. For example, parrots have been taught to respond to instructions from humans using words of English vocabulary, and to respond to simple questions by combining several words to form distinctive speech patterns (Todt, 1975; Pepperberg, 1981).

The presence of live tutors also appears to extend the sensitive phase of learning in some species. Young white-crowned sparrows (*Zonotrichia leucophrys*) only learn song from taped conspecific playbacks if they are presented between 10 and 50 days (Marler, 1970), but Baptista and Petrinovich (1986) were able to extend the sensitive phase of learning in the same species by using the more salient stimuli of live tutors.

In many species of birds, a relevant social context appears to be necessary for the proper development of vocalisations. If an appropriate stimulus is not present, learning can be postponed until one is available. When young male zebra finches are deprived of a tutor during the sensitive phase of song learning between 35 to 65 days (Eales 1985, 1987; Clayton, 1987; Slater *et al.*, 1988; Böhner, 1990), they recall elements heard from their father when they were fledglings (Slater *et al.*, 1993). However, birds that had been female raised only and had experienced extreme social deprivation by isolation from 35 to 120 days, demonstrated some degree of vocal plasticity by dropping or gaining elements in their songs when later presented with tutors (Jones *et al.*, in press). Slater *et al.* (1993) also showed evidence that males without adult tutors would partially modify their songs in accordance with the other young males in their group. This shows certain similarities with the process of call convergence that was observed in budgerigars in Chapter 5 and 6, where cagemates copied the calls of one another, but in any event indicates that age-dependent learner species, such as the zebra finch, may have a greater degree of vocal plasticity than earlier studies suggested (e.g. Immelmann, 1969).

In response to the findings of Jones et al. (in press), Chapter 3 investigated whether there was evidence of vocal plasticity in the learning of calls as well as song. The DC of

the zebra finch is thought to be at least partially learnt during a sensitive phase prior to song learning, before 40 days of age. Zann (1985) found that the template for the acquisition of the normal DC of male zebra finches is open to certain environmental influences. Most males appear to inherit specifications of the noise element of the DC (the most sexually diagnostic feature of the call), but an appropriate model is needed for normal modulation to occur after day 40.

The results of Chapter 3 provided no evidence that normally raised zebra finches can learn calls in adulthood, despite the possibility that close proximity to live interactive conspecifics may have provided a more salient stimulus. Even in those birds that were female raised and therefore deprived of an appropriate adult male tutor, there was no change in the calls in adulthood. The presence of a normal adult male tutor in a third group did not appear to result in any change either.

Chapter 2 examined the possible contribution of genetic and environmental influences in shaping the characteristics of the zebra finch DC. It has already been shown that the DCs of male zebra finches are prone to be influenced by their social environment, particularly during a sensitive phase early in their development (Brindley, 1988; Jones, 1994; Immelmann, 1969, 1972; ten Cate, 1982; Zann, 1984, 1985). Some of these studies have suggested that call learning occurs prior to the sensitive phase of song learning (Brindley, 1988; Zann, 1985) with the possible implication that young birds may base their choice of song tutor on whether or not it calls like the young bird's father did. However, Slater and Jones (1995) found no evidence from their results that the DC was learnt earlier and the song later; DCs were not learnt from the father to a greater extent than song. This raises the question of whether or not calls are likely to reflect kinship.

Zann's study (1985) certainly appeared to indicate a strong tendency for the DCs of male zebra finches to reflect kinship; some 30% of normally reared males gave DCs

that were identical to those of their fathers whilst the remainder showed strong resemblance's to them. Of young males that had been cross-fostered, 16% learnt the DC of their Bengalese finch foster father. Zann (1990) also found that in the wild, within a family, DCs were conserved more strongly than song down the generations, but Slater and Jones (1995) caution that this may be because DCs are less variable and therefore more likely to be matched and transmitted without copying errors.

The results of Chapter 2 appear to reflect those of Zann (1985) in that sons are likely to be closer in the characteristics of their DCs to the male that raised them and the male nest mates they were raised with than any other birds. This alone suggests that calls are learnt and that they are acquired prior to day 50, which is when birds are removed from their fathers. Genetic fathers that had raised their offspring were found to be more similar in their calls than foster fathers and sons. At first, this may appear to be an indication that calls are, at least in part, inherited, but there are likely to be many other factors involved in the acquisition of calls, such as differences in parental contact with the offspring and differing levels of vocalising between parents and young.

The significance of call convergence in social flocking species has been the subject of some speculation (Farabaugh *et al.*, 1994; Mammen & Nowicki, 1981; Mundinger, 1970; Nowicki, 1989; Thorpe & North, 1966). The question that remains is what possible function or advantage could there be in sharing the same call as all other individuals within a social group. The suggestion that shared contact calls could act as a badge of group membership (Treisman, 1978), and aid in the synchronisation and co-ordination of the movements and activities of group members (Farabaugh et al., 1994) all seem to be feasible advantages to possessing a group specific call, but it is unlikely that these provided an initial selective pressure for some species to undergo call convergence.

Chapter 6 examined the process of call convergence, but unlike Chapter 5, which studied the affect of various social factors in determining which birds were copied and to what extent, particular attention was concentrated on whether imitation was mutual in a group with an asymmetric social status. Previous studies on species that undergo call convergence, most relevantly those on black-capped chickadees (Mammen & Nowicki, 1981; Nowicki, 1989) and budgerigars (Farabaugh, et al., 1994), have reported that convergence occurred through a process of mutual imitation with no particular individuals emerging as copiers or tutors. It seems unlikely that all individuals contribute equal input in to the production of a new group specific call, in which case certain birds may initiate a new call while other conform to it.

In Chapter 5 there was evidence that individuals that share close social bonds are more similar in their versions of the group call. Indeed, it would be interesting to examine similarities in the calls of mated pairs or siblings because of their close social bonds and proximity to one another within the flock. The shortcomings of the experiments of Nowicki (1989) and Farabaugh (1994) were that all individuals were familiar with each; an unlikely situation in a wild flock in which recruitment probably occurs over a prolonged period. This means that new individuals are more likely to encounter birds with established social bonds and, bearing in mind that the influence of social factors in vocal learning, it is probable that this will affect the process of call convergence.

Chapter 6 found that call convergence does not arise through mutual imitation when new recruits are introduced to an established flock with a group specific call. Instead, it is the new recruit which converges almost entirely on the group specific call of the established flock members. This would tend to suggest that call convergence functions as a means of social facilitation and integration into the flock.

It is possible that unfamiliar individuals learn the group specific call in appeasement so that they may be accepted into the group and formulate social bonds with its members,

or alternatively, new recruits could form social bonds and then, as a result of being more intimate, develop an identical call to their new flock mates. This cause or effect issue is difficult to answer without considering the social behaviours and relationships of flock mates more closely.

An interesting consequence of call sharing in social groups is the apparent constraints it would place on individual recognition. An experiment could be performed which tested an individual's ability to discriminate familiar flockmates, based on the playback of the individual renditions of the same group specific call. Individuals do not obviously produce absolutely identical copies of the group call, but fairly sensitive auditory capabilities would be needed to recognise individuals from one common shared call.

Playback discrimination tests are also needed to determine the extent to which the DC of zebra finches can be used in individual recognition and to investigate the potential for use in kin recognition. Female zebra finches could be tested with sequential playbacks of the DCs of familiar and unfamiliar, and related and unrelated zebra finches, to observe if discrimination can occur. DCs do appear to be more similar within families than between families (Zann, 1985), but some studies have shown that the choice of call tutor may not be as clear cut as simply copying the father as appears to be the case with song learning too (Slater & Jones, 1995).

Experiments are needed to examine the potential for parent-offspring recognition based on contact calls of both zebra finches and budgerigars, and, if parents can recognise offspring (and *vice versa*), and if so, at what age this occurs in the young birds' development. Studies on the interaction between visual and auditory cues in vocal learning would also be worthwhile, such as those of Trillmich (1976).

Caution should be made in extending the findings of laboratory experiments to explain the functional significance of behaviours in the wild. These experiments are obviously

very artificial and cannot realistically be justified as being homologous with a natural situation. The most detailed studies of parrot vocal communication have been performed in the laboratory, including studies of perception, production, and development of learned vocalisations (e.g. Dooling et al., 1987a-b; Farabaugh *et al.*, 1992, 1994; Pepperberg, 1990; Todt, 1975). However, more often than not, the species that have been studied in the field have not been studied in the laboratory and *vice versa*. Detailed laboratory and field studies of the same species would provide the necessary background data to enable a thorough comparison of vocal learning in parrots with that in songbirds.

Field playback experiments of budgerigar vocalisations could reveal important contextual variables that operant laboratory studies have missed (Falls, 1987), but would lack the control of laboratory experiments. Though budgerigars can learn new vocalisations throughout adulthood, vocal learning begins early in life, and it would therefore be interesting to study the effect of cross-fostering on the development of vocal learning later in life.

Previously, neuro-anatomical studies of vocal learning have excluded call learning, choosing instead to concentrate on the song learning of oscine species, and yet, in the zebra finch at least, the learning of calls and song involves the same neural pathways (Simpson & Vicario, 1990). The neural circuitry of the budgerigar auditory and vocal motor pathways differ from those in songbirds (Brauth *et al.*, 1987), and vocal learning in the two taxa probably arose independently. Comparative experimental and neurological studies of open-ended vocal learning in adulthood of psittacines such as the budgerigar, and the more age-limited learning oscine species such as the zebra finches, would provide interesting perspectives on the studies of the evolution of vocal learning in birds.

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Appendix 2.1 Sonagraphic analysis

A.2.1.1 Sound similarity

Sound comparison has traditionally been performed by visual estimates from spectrograms or by statistical comparisons of measured sound parameters (e.g. maximum and minimum frequency, time of peak frequency, frequency slope, etc.). Visual comparison is comprehensive, but lacks objectivity, repeatability, and mathematical universality. Extracted sound parameters are mathematical, but may not capture sufficient detail to represent a complex sound, and are inherently biased by parameter choice.

SIGNAL sound similarity addresses these limitations. It is based on the quantitative comparison of sound functions (e.g. amplitude envelopes, power spectra, spectral contours, or spectrograms). Unlike visual techniques, the comparison is quantitative and objective, based on the cross-correlation function, while unlike sound parameters, sound functions have the capacity to represent sound characteristics in considerably more detail than individual sound parameters.

A.2.1.2 Sound functions

SIGNAL sound comparison is based on transforming a sound to a sound function that represents one or more of its acoustic features. Sound comparison is performed on an entire sound set by transforming all sounds this way, then comparing the sound functions

quantitatively. Different sound functions represent different sound features. Amplitude envelopes can represent time-varying intensity, gate functions can represent pulse-repetition temporal patterns, spectral contours can represent time-varying dominant frequency, power spectra can represent total average spectral distribution, and spectrograms can represent frequency altering over time.

In order to analyse a sound set for broadest similarity, spectrograms are used to compare almost all sound features at once. These results don't reveal which 'fine-grain' features contribute to the resulting similarity (though visual post-inspection may reveal this). Alternatively, to investigate the similarity significance of a single sound feature, a more restricted and well-defined sound function can be employed, such as the average power spectrum or amplitude gate.

A.2.1.3 Generalised similarity technique

SIGNAL's generalised similarity technique involves three steps:

1. Convert the sound set to sound functions (e.g. spectrograms).
2. Calculate pairwise quantitative similarity between all sound functions by aligning spectrograms on the time axis. Assemble these similarities as a triangular matrix of normalised (0-1) similarity values.
3. Analyse the similarity matrix for any differences, using one of several statistical approaches (e.g. multi-dimensional scaling (MDS) or bootstrapping).

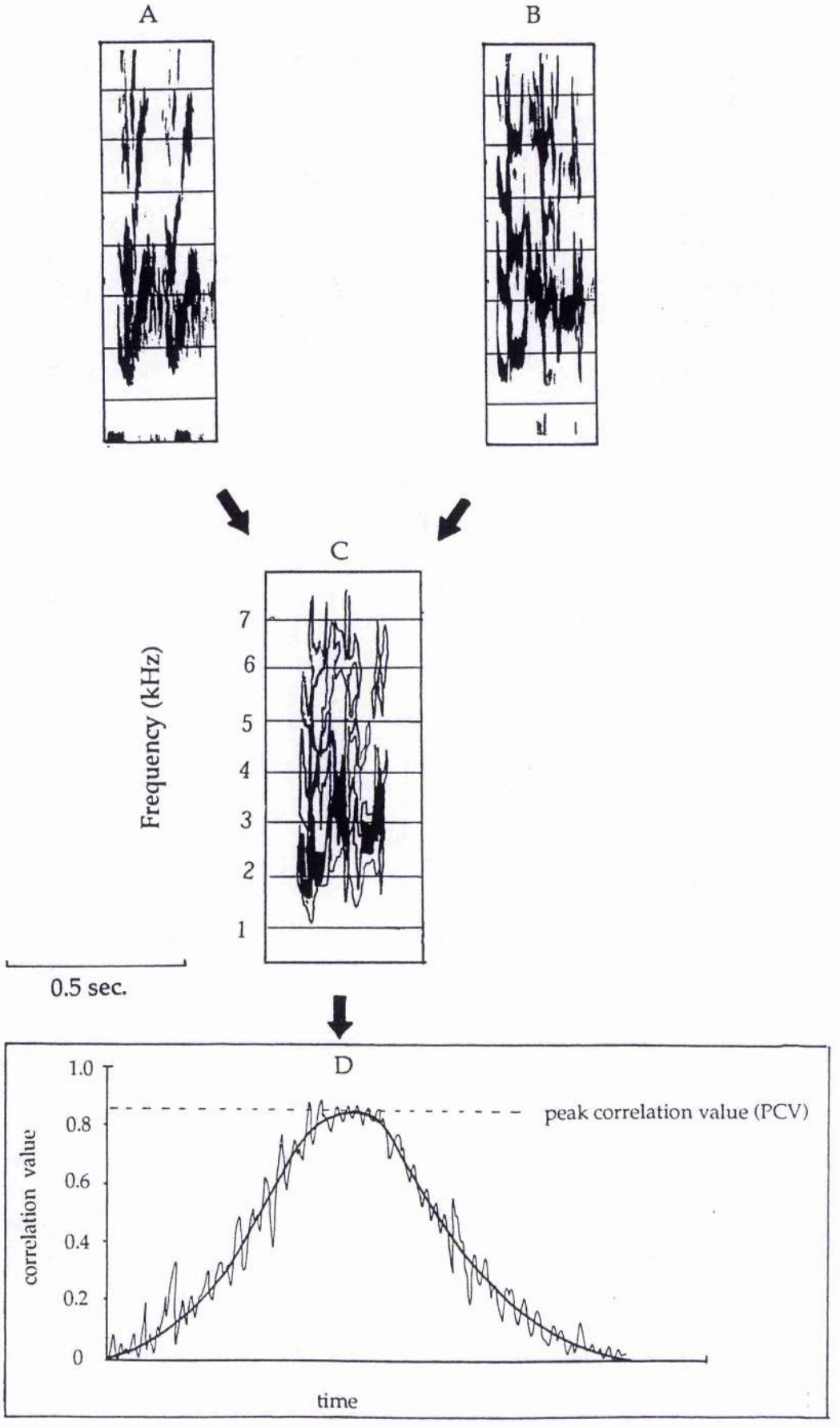
Step 1 involves the formulation of a sound function that represents the sound feature to be compared (in this case the formulation of digital spectrogram). Step 2 involves pairwise cross-correlations between the derived sound functions. Step 3 is performed outside of SIGNAL, using statistical analysis software (e.g. SPSS or Minitab).

A.2.1.4 Limitations of the spectrogram comparison technique

The spectrogram comparison technique measures the degree of physical overlap between two spectrograms. It overlays the spectrograms and statistically 'counts' the common squares (see Fig A.2.1). Unlike parametric comparisons, this technique retains the full spectrographic detain of the sound. For this reason, it provides the most sensitive measure of similarity between sounds that are nearly similar. To the extent that physical overlay is a sufficient measure of morphological similarity, this technique is excellent. However, the spectrogram comparison technique does not measure 'conceptual similarity' (i.e. sounds that are similar conceptually but not within the mathematical constraints of the spectrogram comparison technique):

1. **Time constraints**: consider two sounds of similar spectral shape that differ in the time duration. The reported similarity will reflect the low degree of time congruence rather than the high degree of shape similarity.
2. **Frequency transformations**: consider two sounds of similar spectral shape that differ in absolute frequency. Again, the reported similarity will reflect the low degree of frequency congruence, rather than the high degree of shape similarity. This is taken care of by spectrogram frequency shifting.

Fig A.2.1 Simplified schematic representation of the sequences of events involved in cross-correlation analysis. Two digital spectrograms of calls (A and B) are overlayed one another (C). The dark shaded area represents the common area of maximum overlay between the two spectrograms and is the point where the peak correlation value (PCV) is obtained. The spectrograms are moved over one another in the time domain and a sequence of correlation values taken at regular intervals (D). The peak of the graph represents the PCV where the overlay between the two spectrograms is greatest.


A
B
C
7
6
5
4
3
2
1
Frequency (kHz)
0.5 sec.
D
1.0
0.8
0.6
0.4
0.2
0
correlation value
peak correlation value (PCV)
time

3. **Harmonic material**: the spectrogram technique works best with tonal material and least with harmonic or 'noisy' sounds. Consider two sounds, each containing multiple harmonics. If the fundamentals differ by 10% and all other features are similar, then the two 5^{th} harmonics will differ in frequency by 50%, and the overlap of the harmonics will be limited severely, reducing the computed spectrogram similarity. This limitation can be addressed by limiting the spectrogram frequency range to the fundamentals, or more effectively, the sounds can be converted to spectral contour functions, normalised for differences in fundamental frequency, and similarity can be computed between the contours rather than spectrograms.

A.2.2 Bootstrapping statistical analysis

The PCV results of cross-correlation analysis are very suitable for detecting similarities between two digitised sonagrams of calls, but standard non-parametric methods cannot be employed to statistically test the data because of its dependent nature. An alternative method of testing these results is therefore needed.

Bootstrapping analysis is suitable for testing dependent data. It involves the multiple random resampling of a data set to produce a random distribution to which the original set is compared. In order to clarify this process, an example of the methodology is given below.

Population 1	Population 2	Pop^n1+Pop^n2	Random 1	Random 2
2	5	2	5	6
6	4	6	1	5
1	5	1	2	3
3	3	3	6	2
3	6	3	3	4
2	5	2	5	3
		5		
		4		
		5		
		3		
		6		
		5		
2.8	4.7		3.7	3.8

Above is a spread sheet for a hypothetical data set consisting of two populations for comparison (population 1 and population 2). The third column ($Pop^n1+ Pop^n2$) represents how the data are entered into Minitab statistical package prior to bootstrapping. The software now considers the two populations as one. Bootstrapping involves the formulation of two populations from a random selection of the $Pop^n1 + Pop^n2$ column, and the difference between the means of the two new random populations calculated. This procedure is repeated however many times are desired, usually between 500 and 1000 times. A new normal distribution is then constructed from

the differences between the means. The difference in the means of the original populations is then compared to the random distribution. If the value falls within the random distribution, then the two populations are themselves concluded to be random and there is no significant difference between them.

After bootstrapping, the following values are given to represent the comparison:

	N	MEAN	ST. DEV.	SE. MEAN
data	100	0.1500	0.9527	0.0953

A z-score can be calculated from the comparison between two populations.

$$\frac{\text{(difference between means or original pop}^{n}\text{) - mean from bootstrapping}}{\text{standard deviation from bootstrapping}}$$

$$z = 1.83$$

In this case the z-score is below the threshold value of 1.96 for P=0.05, and we can conclude that there is no significant difference between the two populations.